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## GLOSSARY

- AELIACTA**: animals without shell (*coelomata*)  
**ANTRIOMERISM**: the condition (*genus*) of  
man (*anthropos*)  
**ANTHROPOLOGY**: the science of man  
**ANUS**: (in compounds) the seat or typical  
exit, arche-anus, archi-gastrula, etc.
- ARCHIPLATE**: the nucleus of the gonova of life  
(*archi*)
- BLAST-**: (in compounds) pertaining to the  
early embryo (*blastis* = a bud); hence —
- Blastoderm**, skin (*derma*) or enclosing  
layer of the embryo
- Blastosphere**: the embryo in the  
hollow sphere stage
- Blastula** name for preceding
- Hypoblast**: The outer layer of the  
embryo (ectoderm)
- Hypoblast**: the inner layer of the  
embryo (endoderm)
- BREVICHTHAL**: pertaining to the fifth  
(brevis) chitinous band
- CHEMIS**: (in compounds) pertaining to the  
nucleus (*cytus*), hence —
- CHEMOTAXON**: the movement of the  
nucleus
- CHELYDYL**: dissipation of the nucleus
- CHELYDYLIN**: the matter of the nucleus
- CYTOSTRUCTURE**: see under LECTURE
- CYCLOPES and CHILOPODES**: animals with a  
dorsal chord or back-bone
- LATRE or CHILOPODES**: the body-cavity in the  
embryo; hence —
- CALOPODIA**: animals without a body-  
cavity
- CELIOMATA**: animals with a body-  
cavity
- COCHEOMERISM**: formation of the body-  
cavity
- CYTO-**: (in compounds) pertaining to the  
cell (*cytus*); hence —
- CYTOBLAST**: the nucleus of the cell
- CYTODES**: cell-like bodies, imperfect  
cells
- Cytoplasm**: the matter of the body of  
the cell
- Cytosoma**: the body ( *soma*) of the cell
- CYTOSTRUCTURE**: abnormal retention of the  
nucleus in the body
- DACTYLOPLASM**: see PLATE
- DIATOM**: the belief in the existence of two  
entirely distinct protypes (such as matter  
and spirit)
- DYSTELOLOGY**: the science of those  
features in organisms which refute the  
"design-argument."
- EXOBLAST**: the outer (*exos*) layer of the  
embryo
- EXOBlast**: the inner (*endo*) layer of the  
embryo
- EXOBlast**: the outer layer of the vein
- EXOGENY**: the theory of gradual develop-  
ment of organs in the embryo
- EXOPHRYS**: the third or central eye in the  
early vertebrates
- EXOPLASMA**: see SODA
- EXOCRINAE**: glands covering the surface of  
parts of the body (such as the mouth, etc.)
- EXOCRINE**: the sexual glands
- EXOCRINOSIS**: separation of the male and  
female sexes
- EXOCRINOSIS**: sections of the sexual glands
- EXOCRINOUS**: a male with the breasts  
(*female*) of a woman (*figae*)
- EXOTERIC**: pertaining to the liver (*hepatis*)
- HOMOBLASTIC**: embryo in which the animal  
and vegetal cells divide equally (*whole* or  
*whole*)
- HOMOBLASTOSIS**: the possession of more  
than the normal breed (*crews*)
- HOMOBLASTOSIS**: underneath (*hyle*) the  
gill
- HOMOPHYL**: sprout-offshoot from the  
body in the primitive vertebrates
- HYPOMORPH**: see SODA

<b>LACERTA:</b> pertaining to the yolk ( <i>lacertifer</i> );— head;— Centrocercal: eggs with the yolk in the centre Locithora: the yolk-sac Telolecithal: eggs with the yolk at one end	<b>Corytoplasm:</b> the matter of the nucleus ( <i>caryoplasm</i> ) <b>Cytoplasm:</b> the matter of the body of the cell <b>Dermoplast:</b> secondary or differentiated plasma <b>Mesoplasm:</b> same as preceding <b>Protoplasm:</b> primitive or undifferentiated plasma
<b>MEROMELATRIC:</b> cleaving in part ( <i>meromes</i> ) only <b>MET-</b> : (in compounds) the "after" or secondary stage; hence:— Metagenetic: the secondary or permanent gut ( <i>gaster</i> ) Metaplastic: secondary or differentiated plasma Metamorph: the secondary or permanent mouth ( <i>stomach</i> ) Metamere: the higher or later embryo, made up of many cells Metamorphosis: the process of enhanced growth <b>MERISTEAT:</b> the segments into which the embryo breaks up <b>MESOTHEM:</b> the segmentation of the egg before <b>MESOTHEM:</b> the next process of the egg cellular rearrangements Mesosome: belief in the fundamental unity of all things Metamorphosis: the change of regime, regime (generally equivalent to anatomy) <b>MESOTOMIA:</b> segments into which the embryo breaks up	<b>Plasm:</b> the simplest form of plasma <b>PLASTOMER:</b> small particles of plasma <b>POLYMERATION:</b> the penetration of more than one sperm-cell into the ovule <b>PRO- or PATER:</b> (in compounds) the earlier (opposed to MET-) time.— Prothorax: the first or prothoracic segment Prosternon: the first or prosternous sternite Prosternous: the anterior phase of the sternite Prostrophyta: the protists or unicellular plants Protogerm: undifferentiated plasma Protostome: the primitive or ancestral animals
<b>RETICULAR:</b> pertaining to the kidneys ( <i>rete</i> )	
<b>SACRIFICATION:</b> picking or breaking up (scavenging = a verb)	
<b>SACRIFIGURATE:</b> segments into which the primitive vertebrates split	
<b>SCHIZA:</b> the body, hence:— Cytoschiza: the body of the cell ( <i>caryoplasm</i> )	
<b>SCHIZOCYST:</b> the upper or back-half of the embryonic body	
<b>SCHIZOCYST:</b> segment of the embryonic body	
<b>HYPONOTUS:</b> the under or belly half of the embryonic body	
<b>TELEOLOGY:</b> the belief in design and purpose (of life) in nature	
<b>TRIPLER:</b> three times the size.	
<b>UNICELLULAR:</b> pertaining to the nuclei ( <i>uni-</i> celles)	
<b>VITELLINUS:</b> pertaining to the yolk ( <i>vitellifer</i> )	

## PREFACE

[By JOSEPH McCARR]

The work which we now place within the reach of every reader of the English tongue is one of the finest productions of its distinguished author. The first edition appeared in 1874. At that time the conviction of man's natural evolution was even less advanced in Germany than in England, and the work raised a storm of controversy. Theologians—forgetting the commonest facts of our individual development—spoke with the most profound disdain of the theory that a Luther or a Goethe could be the outcome of development from a tiny speck of protoplasm. The work, one of the most distinguished of them said, was "a flock of shams on the countechein of Germany." To-day its conclusion is accepted by influential clerics, such as the Dean of Westminster, and by almost every biologist and anthropologist of distinction in Europe. Evolution is not a laboriously reached conclusion, but a guiding truth, in biological literature to-day.

There was ample evidence to substantiate the conclusion even in the first edition of the book. But fresh facts have come to light in each decade, always enforcing the general truth of man's evolution, and at times making clearer the line of development. Professor Haeckel embodied these in successive editions of his work. In the fifth edition, of which this is a translation, reference will be found to the very latest facts bearing on the evolution of man, such as the discovery of the remarkable effect of mixing human blood with that of the anthropoid ape. Moreover, the ample series of illustrations has been considerably improved and enlarged; there is no scientific work published, at a price remotely approaching that of the present edition, with so abundant and excellent a supply of illustrations. When it was issued in Germany, a few years ago, a distinguished biologist wrote in the *Frankfurter Zeitung* that it would secure immortality for its author, the most notable critic of the idea of immortality. And the *Daily Telegraph* reviewer described the English version as a "handsome edition of Haeckel's monumental work," and "an issue worthy of the subject and the author."

The influence of such a work, one of the most constructive that Haeckel has ever written, should extend to more than the few hundred readers who are able to purchase the expensive volumes of the original issue. Few pages in the story of science are more arresting and generally instructive than this great picture of "mankind in the making." The horizon of the mind is healthily expanded as we follow the search-light of science down the vast avenues of past time, and gaze on the unsmooth forms that enter

into, or illustrate, the line of our ancestry. And if the imagination recoils from the strange and remote figures that we fit up by our search-light, and hesitates to accept them as ancestral forms, science draws aside another veil and reveals another picture to us. It shows us that each of us passes, in our embryonic development, through a series of forms hardly less uncouth and unfamiliar. Nay, it traces a parallel between the two series of forms. It shows us man beginning his existence, in the ovary of the female infant, as a minute and simple speck of jelly-like plasma. It shows us (from analogy) the fertilised ovum breaking into a cluster of cohering cells, and folding and curving, until the limb-less, head-less, lung-tailed fetus looks like a worm-shaped body. It then points out how gill-slits and corresponding blood-vessels appear, as in a larval fish, and the fin-like extremities bud out and grow into limbs, and so on; until, after a very clear ape-stage, the definite human form emerges from the series of transformations.

It is with this embryological evidence for our evolution that the present volume is concerned. There are illustrations in the work that will make the point clear at a glance. Possibly no clearer for the simplicity of the idea and the sagacity to apply it at every point have carried many, who borrow hastily from Haeckel, out of their scientific depth. Haeckel has never shared their errors, nor encouraged their superficiality. He insists from the outset that a complete parallel could not possibly be expected. Embryonic life itself is subject to evolution. Though there is a general and substantial law—as some of our English and American authorities admit—that the embryonic series of forms recalls the ancestral series of forms, the parallel is blurred throughout and often distorted. It is not the obvious resemblance of the embryos of different animals, and their general similarity to our extinct ancestors in this or that organ, on which we must rest our case. A careful study must be made of the various stages through which all embryos pass, and an effort made to prove their real identity and therefore genealogical relation.

This is a task of great subtlety and delicacy. Many scientists have worked at it together with Professor Haeckel—I need only name our own Professor Balfour and Professor Ray Lankester—and the scheme is fairly complete. But the general reader must not expect that even so clear a writer as Haeckel can describe these intricate processes without demanding his very careful attention. Most of the chapters in this present volume (and the second volume will be less difficult) are easily intelligible to all; but there are points in which the line of argument is necessarily subtle and complex. In the hope that most readers will be induced to master even these more difficult chapters, I will give an outline of the characteristic argument of the work. Haeckel's distinctive services in regard to man's evolution have been: (1) The construction of a complete ancestral tree, though, of course, some of the stages in it are purely conjectural, and not final; (2) The tracing of the remarkable reproduction of ancestral forms in

the embryonic development of the individual. Naturally, he has not worked alone in either department. The second volume of this work will embody the first of these two achievements; the present one is mainly concerned with the latter. It will be useful for the reader to have a synopsis of the argument and an explanation of some of the chief terms invented or employed by the author.

The main theme of the work is that, in the course of their embryonic development, all animals, including man, pass roughly and rapidly through a series of forms which represents the succession of their ancestors in the past. After a severe and extensive study of embryonic phenomena, Haeckel has drawn up a "law" (in the ordinary scientific sense) to this effect, and has called it "the biogenetic law," or the chief law relating to the evolution (*genetik*) of life (*Leben*). This law is widely and increasingly accepted by embryologists and zoologists. It is enough to quote a recent declaration of the great American zoologist, President D. Starr Jordan: "It is, of course, true that the life-history of the individual is an epitome of the life-history of the race"; while a distinguished German zoologist (Darwin) has described it as being of the same use to the biologist as "spectrum analysis is to the astronomer."

But the reproduction of ancestral forms in the course of the embryonic development is by no means always clear, or even always present. Many of the embryonic phases do not recall ancestral stages at all. They may have done so originally, but we must remember that the embryonic life itself has been subject to adaptive changes for millions of years. All this is clearly explained by Professor Haeckel. For the moment, I would impress on the reader the vital importance of fixing the distinction from the start. He must thoroughly familiarise himself with the meaning of five terms. *Ontogeny* is the development of life in general (both in the individual and the species), or the science describing it. *Ontogeny* is the development (embryonic and post-embryonic) of the individual (*sae*), or the science describing it. *Phylogeny* is the development of the race or stem (*phylum*), or the science describing it. Roughly, *ontogeny* may be taken to mean embryology, and *phylogeny* what we generally call evolution. Further, the embryonic phenomena sometimes reproduce ancestral forms, and they are then called *homoplastic* (from *plus* = again); sometimes they do not recall ancestral forms, but are later modifications due to adaptation, and they are then called *convergent* (from *versus* = new or foreign). These terms are now widely used, but the reader of Haeckel must understand them thoroughly.

The first five chapters are an easy account of the history of embryology and evolution. The sixth and seventh give an equally clear account of the sexual elements and the process of conception. But some of the succeeding chapters must deal with embryonic processes so unfamiliar, and pursue them through so wide a range of animals in a brief space,

that, in spite of the 200 illustrations, they will offer difficulty to many a reader. As our aim is to secure, not a superficial acquiescence in conclusions, but a fair comprehension of the truths of science, we have retained these chapters. However, I will give a brief and clear outline of the argument, so that the reader with little leisure may realize their value.

When the animal ovum (egg-cell) has been fertilized, it divides and sub-divides until we have a cluster of covering cells, externally not unlike a raspberry or mulberry. This is the *morula* (= mulberry) stage. The cluster becomes hollow, or filled with fluid in the centre, all the cells rising to the surface. This is the *blastula* (hollow ball) stage. One half of the cluster then bends or folds in upon the other, as one might do with a thin Indianrubber belt, and we get a vase-shaped body with hollow interior (the first stomach, or "primitive gut"); an open mouth (the first or "primitive mouth"); and a wall composed of two layers of cells (two "gastric layers"). This is the *gastrula* (stomach) stage, and the process of its formation is called *gastrulation*. A glance at the illustration on p. 6; will make this perfectly clear.

So much for the embryonic process in itself. The application to evolution has been a long and laborious task. Briefly, it was necessary to show that all the vertebrate animals passed through these three stages, so that our biogenetic law would enable us to recognize them as reminiscences of ancestral forms. This is the work of Chaps. VIII. and IX. The difficulty can be realized in this way: As we reach the higher animals the ovum has to take up a large quantity of yolk, on which it may feed in developing. Think of the bird's "egg." The effect of this was to flatten the germ (the morula and blastula) from the first, and so gives, at first sight, a totally different complexion to what it has in the lower animals. When we pass the reptile and bird stage, the large yolk almost disappears (the germ now being supplied with blood by the mother), but the germ has been permanently altered in shape, and there are now a number of new embryonic processes (membrane, blood-vessel connections, etc.). Thus it was no light task to trace the identity of this process of *gastrulation* in all the animals. It has been done, however; and with this introduction the reader will be able to follow the proof. The conclusion is important. If all animals pass through the curious gastrula stage, it must be because they all had a common ancestor of that nature. To this conjectural ancestor (it lived before the period of fossilization begins) Haeckel gives the name of the *Gastraea*, and in the second volume we shall see a number of living animals of this type ("gastrapoda").

The line of argument is the same in the next chapter. After laborious and careful research (though this stage is not generally admitted in the same sense as the previous one), a fourth common stage was discovered, and given the name of the *Cnidaria*. The blastula had one layer of cells, the *Hæcderma* (*derma* = skin); the gastrula two layers, the *ectoderm* ("outer skin"); and *entoderm* ("inner skin"). Now a third layer (*mesoderm*)

—middle skin) is formed, by the growth inwards of two pouches or folds of the skin. The pouches bleed together, and from a single cavity (the body cavity, or *cavum*), and in two walls are two fresh "germinal layers." Again, the identity of the process has to be proved in all the higher classes of animals, and when this is done we have another ancestral stage, the *Cnidaria*.

The remaining task is to build up the complex frame of the higher animals—always showing the identity of the process (on which the evolutionary argument depends) in enormously different conditions of embryonic life—out of the four "germinal layers." Chap. IX. prepares us for the work by giving us a very clear account of the essential structure of the back-boned (vertebrate) animal, and the probable common ancestor of all the vertebrates (a small fish of the lamprey type). Chaps. XI.—XIV. then carry out the construction step by step. The work is now simpler, in the sense that we leave all the invertebrate animals out of account; but there are so many organs to be fashioned out of the four simple layers that the reader must proceed carefully. In the second volume each of these organs will be dealt with separately, and the parallel will be worked out between its embryonic and its phylogenetic (evolutionary) development. The general reader may wait for this for a full understanding. But in the meantime the wonderful story of the construction of all our organs in the course of a few weeks (the human frame is perfectly formed, though less than two inches in length, by the twelfth week) from so simple a material is full of interest. It would be useless to attempt to summarize the process. The four chapters are themselves but a summary of it, and the eighty fine illustrations of the process will make it sufficiently clear. The last chapter carries the story on to the point where man at last parts company with the anthropoid apes, and gives a full account of the membranes or wrappers that enfold him in the womb, and the connection with the mother.

In conclusion, I would urge the reader to consult, at his free library perhaps, the complete edition of this work, when he has read the present abbreviated edition. Much of the text has had to be condensed in order to bring out the work at our popular price, and the beautiful plates of the complete edition have had to be omitted. The reader will find it an immediate assistance if he can consult the library edition.

Josiah McCance.

Oxford, March, 1905.

## HAECKEL'S CLASSIFICATION OF THE ANIMAL WORLD.

#### **Verbalizing methods (continued)**

- |                |                                  |                                |
|----------------|----------------------------------|--------------------------------|
| 2. Univoltine  | { Diurnal<br>Prothomolous }      | } Diurnal                      |
| 3. Bivoltine   | { a. Diapause<br>b. Polyphagy }  | { Anisotrophic<br>Bivoltine }  |
| 3. Cetivoltine | { Catadromous<br>Heterochroism } | { Polyphagous<br>Cetivoltine } |

#### **Reaktionen mit dem Wasserstoff**

- |                                 |   |
|---------------------------------|---|
| a. Ciliaten                     | 1. Ciliata  |
| b. Spangen                      | 2. Stramenopiles  |
| c. Ciliatidae<br>(ungeschwämmt) | 3. Heterokontophytes  |
| d. Plankton<br>(heit-werden)    | 4. Hydrozoa   |
| e. Vertebrata<br>(spindelbeine) | 5. Radiata  |
| f. Mollusca                     | 6. Annelida   |
| g. Articulata                   | 7. Echinodermata  |
| h. Entomophora                  | 8. Brachiopoda  |
| i. Trichoplanteae               | 9. Bryozoa  |
| j. Vertebrates                  | 10. Thallophytes  |
| k. Fische                       | 1. Actinopteroides<br>- radiata subcl.                                      |
| l. Crustacea                    | 2. Crustacea<br>- radiata subcl.<br>a. Copepodida<br>("pseudoscrutellidae") |
| m. Vertebrates                  | 3. Osteichthyes   |

### *6. Vertebrates*

- | "so-called-mosquitoes" |   |
|------------------------|---|
| A. <i>Stegomyia</i>    | Palau fly<br>Lutetianid<br>Takaoensis<br>Supernigra   |
| B. <i>Anopheles</i>    |   |
| C. <i>Repinella</i>    |   |
| D. <i>Rhodomyia</i>    |   |
| E. <i>Mosquitos</i>    | Monopteron<br>Mansonioides<br>Flavostriatus<br>Rufipes<br>Bimaculata<br>Univittata<br>Cotocaera<br>Pertusa<br>Inornata<br>Elatocarpis<br>Carminea<br>Prinomia |

*Ctenophorus*,  
*Diplodactylus*, &  
Scaphiopus.  
Anuridae with  
body cavity, blood  
or mucus.

**II**  
**Classification of  
Minerals.**

This information is given for the purpose of guidance. Standard - 100% of course in this subject. The student may take as much time as he wishes to complete his work. He must submit his work to the teacher for examination.

# THE EVOLUTION OF MAN

## CHAPTER I.

### THE FUNDAMENTAL LAW OF ORGANIC EVOLUTION

tal phenomena into which I would introduce my readers in the following chapters has a quite peculiar place in the broad realms of scientific inquiry. There is no object of investigation that touches man more closely, and the knowledge of which should be more acceptable to him, than his own frame. But among all the various branches of the natural history of mankind, or anthropology, the story of his development by natural means must surely the most fascinating. It gives us the key of the great world-edition at which the human crew has been working for thousands of years. The problem of the nature of man, or the question of man's place in nature, and the cognate inquiries as to the past, the ancient history, the present situation, and the future of humanity—all these none so important questions are directly and satisfactorily connected with that branch of study to which we call the science of the evolution of man, or, in one word, "Anthropogeny" (the genesis of man). Yet it is an astonishing fact that the science of the evolution of man does not even yet form part of the scheme of general education. In fact, educated people even in our day are for the most part quite ignorant of the important truths and remarkable phenomena which anthropogeny teaches us.

As an illustration of this curious state of things, it may be pointed out that some of what are considered to be "educated" people do not know that every human being is developed from an egg, or ovum, and that this egg is one simple cell, like any other plant or animal egg. They are equally ignorant that in the course of the development of this tiny, round egg-cell there is first formed a body that is totally

different from the human frame, and has not the remotest resemblance to it. Most of them have never seen such a human embryo in the earlier period of its development, and do not know that it is quite indistinguishable from other animal embryos. At first the embryo is no more than a round cluster of cells, then it becomes a simple hollow sphere, the wall of which is composed of a layer of cells. Later it approaches very closely, at one period, to the anatomic structure of the larva, afterwards to that of a fish, and again to the typical build of the amphibia and mammals. As it continues to develop, a form appears which is like those we find at the later stage of mammal-life (such as the shrews), then a form that resembles the marsupials, and only at a late stage a form that has a resemblance to the ape. ~~and~~ <sup>and</sup> at last the definite human form emerges and closes ~~a~~ a series of retransformations. These suggestive facts are, as I said, still almost unknown to the general public—so completely unknown that, if one casually mentioned them, they are called in question or denied outright as fancies. Everybody knows that the butterfly emerges from the pupa, and the pupa from a quite different thing called a larva, and the larva from the butterfly's egg. But few besides radical men are aware that man, in the course of his individual formation, passes through a series of transformations which are not less surprising and wonderful than the familiar metamorphoses of the butterfly.

The mere description of these remarkable changes through which man passes during his embryonic life should arouse considerable interest. But the mind will experience a far keener satisfaction when

we turn from science back to their science, and when we have to think in the narrow phenomena which are of the highest importance throughout the whole field of human knowledge. They throw light first of all on the "natural history of creation," then on physiology, or "the causes of the work," and finally this on the whole of philosophy. And as the general results of every branch of inquiry are summed up in physiology, all the sciences come in here to be studied and influenced more or less by the study of the evolution of man.

But when I say that I propose to present here the most important aspects of these phenomena and how close is their stamp, I take the word, and I interpret my title, in a very much wider sense than is usual. The features which have been discussed on this subject in the universities during the last half-century are almost exclusively adapted to medical men. Certainly, the medical men have the greatest interest in studying the origin of the human body, such as it is usually supposed. But I mean not give here that special description of the embryonic processes such as it has hitherto been given, as none of my readers have any medical anatomy, and are not likely to be interested with the more of the whole subject. I mean rather myself with giving some parts of the subject only in general outline, and more or less upon all the approaches, but very intricate and not easily described, details that are found in the story of the development of the human frame. To understand these fully a knowledge of anatomy is needed; I will endeavour to be as plain as possible in dealing with this branch of science. Indeed, a sufficient general idea of the stories of the anterior and posterior of man can be obtained without going too deeply into the anatomical details. I tried my very best to secure the more interest in this difficult field of inquiry, as has been pointed already at other branches of science; though we shall soon make exceptions here than elsewhere.

The story of the evolution of man, as it has hitherto been explained to medical students, has usually been confined to embryology—more correctly, ontogeny—in the science of the development of the individual human embryo. But this is only the first part of our task, the first half of the story of the evolution of man in the wider sense in which we

understand it here. We must add on the second half—an another and not less important and interesting branch of the science of the evolution of the human frame—phylogeny; this may be described as the history of the evolution of the human animal forms, from which the human organism has been developed in the course of successive ages. Everybody now knows of the great novelty of novelty that was exhibited by the publication of Darwin's "Origin of Species" in 1859. The chief direct consequence of this publication was to provide a fresh inquiry into the origin of the human race, and this has passed beyond question our greatest education from the older species. We give the name of "Phylogeny" to the science whose description that gives of man from the top of nature of the created world. The chief weapon that it directs upon for facts is "Ontogeny," or embryology, the science of the development of the individual organism. However, it derives a good deal of support from paleontology, or the science of fossil remains, and even more from comparative anatomy, or morphology.

There two branches of our science—at the one side we go to embryology, and on the other phylogeny, or the history of man—these are now all represented. The one cannot be understood without the other. It is only when the two branches fully complete and supplement each other that "Ontogeny" has the power of the qualities of life in the created world; contrary to the view of a philosophical writer. The connection between them is not external and unimportant, but profound, intimate, and causal. This is a discovery made by recent research, and it is these clearly and naturally expressed in the fundamental law which I have called "the fundamental law of organic evolution," or "the fundamental law of Ontogeny." This general law, in a high and comprehensive manner, occurring, and on the expression of which depends our whole thought over the story of evolution, may be briefly expressed in this form: "The history of the future is a recapitulation of the history of the past"; or, in other words, "Ontogeny is a recapitulation of phylogeny." It may be more fully stated as follows: The series of forms through which the individual organism passes during its development from the ovule to the complete being, appears in a brief, condensed expression,

of the long series of forms which the gradual evolution of the mind, emotion, or the material form of the species, have passed through from the earliest period of animal life down to the present day.

The causal character of the relation which connects phylogeny with ontogeny is due to the nature of heredity and adaptation. When we have rightly understood these, and recognized their great importance in the formation of organisms, we can go a step further and say: Phylogeny is the mechanical law of adaptation. In other words, the development of the tree, or man, is, in accordance with the laws of heredity and adaptation, the cause of all the changes which appear in a descended form in the evolution of the species.

The class of individual animal forms, which represent the ancestry of each higher organism, or race of men, according to the theory of descent, always form a connected whole. We may designate the unbroken series of forms with the letters of the alphabet A, B, C, D, E, etc., to Z. In apparent contradiction to what I have said, the way of the development of the individual — the ontogeny of most organisms, only often to the observer a part of these forms, so that the definition of hereditary factors would read A, B, D, F, H, K, M, etc., or, in other cases, B, D, H, L, M, N, etc. Here, then, as a rule, instead of the evolutionary forms of the individual series have rather run blundered, we often find — to continue with our illustration from the alphabet — one — either of the original letters of the ancestral series represented by corresponding forms from a different alphabet. Thus, writing of the Human B and D, we often have the Greek Ε and Ζ. In this case the tree of the blunderer has here been arrested, just as it had been arrested in the preceding case. But, as yet of all this, the states of arrested forms remain the same, and we are in a position to discern no original connection.

In reality, there is always a certain parallel between the two evolutionary trees. But it is obscured from the fact

that in the embryonic process enough is occurring that certainly cannot be the work of external influences. If the parallel of the two series were complete, and if this great fundamental law affecting the causal connection between ontogeny and phylogeny in the proper sense of the word were directly demonstrable, we should only have to determine, by means of the movements and the observing hand, the series of forces through which the individual animal passes in its development; we should thus have before us a complete picture of the remarkable series of forms which the several authors have always already assumed from the state of organic life down to the appearance of man. But such a representation of the past history by the universal law of heredity, we is very easily imagined. We do not often think of heredity. In most cases the correspondence is very imperfect, being greatly disturbed and hindered by forces which we will consider here. We see then, for the most part, results in dependence on direct, from the study of its embryology, all the different stages which an organism's existence has assumed, as recently and especially in the case of the human fetus—now, many gaps. It is true that we can fill in most of these gaps satisfactorily with the help of comparative anatomy, but we cannot do so from direct heredological observations. Hence it is important that we find a large number of lower animal forms to be still represented, in the course of their embryonic development. In these cases we may draw our conclusions with the greatest certainty as to the nature of the ancestral form from the features of the form which the embryo remanently possesses.

To give a few examples, we can infer from the fact that the human body is a simple cell that the first ancestor of our species was a tiny unicellular living, something like the amoeba. In the same way, we know, from the fact that the human fetus presents, at the first, of course ordinary life processes, that the embryo, a form with few and important parts on the line of our ancestry. A lowly, unicellular form (the amoeba) presents just as clearly as a monkey the embryo (the foetus), the same living condition of which is found among the lowest animals. To give another a more important example, from figure 2, in which we find

<sup>1</sup> The first "series" which every developed animal passes through is the series of the "lower forms." This is the series of the amoeba, the hydra, the rotifer, the larva of the insect, the larva of the fish, the larva of the frog, the larva of the lizard, the larva of the bird, the larva of the mammal, the larva of the man. This is the series of the "lower forms" which every animal passes through, and which every animal has in common with all other animals.

present, in the main, the structure of the habitat. But we can only indirectly and approximately, with the aid of comparative biology and analogy, compare what is or has been done in the chain of our memory between the present and the ultimate, and between that and the former. In the course of the historical development many intermediate structures have a probably false air, which may certainly have been represented in the earlier. That, as regards the mind, and sometimes very appreciably, goes, there is no question; but perhaps the two processes. In fact, as in the chief purpose of this work, to prove the real history and the original possibilities of the race. I hope to show, on a substantial basis of facts, that we can draw most important conclusions as to our comparative past from the stated and analogically derived conditions of analogy. We shall find that it is possible to form a general idea of the modus of animal formation, more figured at the start, and of our memory, in the hunting-habits, of animals.

In this evolutionary apposition of the facts of embryology we must, of course, take particular care to distinguish sharply and clearly between the primitive, pathogenic (or ancestral) evolutionary processes and those due to "adaptation." By "pathogenic processes," or embryonic malformations, we understand all those phenomena in the development of the individual which are transmitted from the gamete to another by heredity, and which, on their account, affect in some degree, whatever be the corresponding structures in the development of the species. On the other hand, we give the name of "adaptive processes," or "adaptive mutations." to all those phenomena in the fetal development that cannot be traced to inheritance from earlier species, but are due to the adaptation of the fetus, or the individual, to certain conditions of its embryonic development. These eugenetic phenomena are foreign to later addition; they allow us to draw no direct inference whatever as to the inheritance of traits in the parental

*Polygynous* are both in proportion to other  
birds.

**History, but either Major or Minor being**

This crucial distinction between the primary or palimpsestic process and the secondary or orthographic is of great importance for the purposes of the historical theory of a species, which has in due course come from the available fields of entomology, comparative anatomy, and paleontology. As to the processes in the formation of the species in the struggle group. It is of the same importance to the writer of entomology as the crucial distinction between genuine and spurious truths in the works of an amateur writer, or the passing of the seal test from interpretation and observation, is for the student of physiology. It is true that this distinction has not yet been fully appreciated by many entomologists. For my part, I regard it as the first condition to forming any just idea of the evolutionary process, and I believe that no one, in accordance with it, divides entomology into two main departments, — the science of morphological forms, and ontogeny, or the science of natural history.

To give at page 8 his statement from the extract of Dr. Cope's article on illustrations of the human skeleton, I may consider the following processes as the outer stage of man, and of all the higher vertebrates as follows:- The formation of the two primary protective layers and of the protective gas. This would bring us out of the dorsal nervous system, the appearance of a simple skin and between the mesodermic tissue and the gas, the temporary separation of the protoplasm and air, the primitive borders and so on. All these, and many other important structures, have already been represented by a steady history from the early members of the mammal, and are, therefore, direct illustrations of the processes of exterior structures in the history of the class. On the other hand, the *inner*, *exterior* and the *inner* life, the hollow and vesicular forms which we now find to be an important process in the formation of the protoplasm, the albumen, the plasma, the nerves, the muscles, and the fibers—or generally speaking, the various secret membranes and the semi-transparent changes in the blood vessels. Perhaps we may see : the *outer* structure of the heart cavity, the *frequency* division of the plates of the primitive envelope and

lateral plates, the secondary closing of the lateral and buccal walls, the formation of the heart, and so on. All these and many other phenomena are certainly not comparable to similar structures in any earlier and comparatively developed animal form, but have arisen simply by adaptation to the peculiar conditions of embryonic life (within the fluid membranes). In view of these facts, we may now give the following more precise expression to the cited law of Hereden. The existence of the heredity (*i.e.* inheritance) is a condition and often leads recapitulation of the evolution of the new (or phylogenetic); and the recapitulation of the more complex or posterior in the original development (or phylogeny) is preserved by a certain fidelity; on the other hand, it becomes less complete in proportion as a varying adaptation to new conditions removes the directing factors in the development (or phylogeny).

The consequent alterations or dislocations of the original phylogenetic course of development like the types, as a rule, of a general displacement of the phenomena, which is surely effected by adaptation to the changed conditions of embryonic evolution during the course of thousands of years. This displacement may take place in regard to either the process or the time of a phenomenon.

The great importance and wide applicability of the terms *adaptation* or *adaptability* have been clearly realized recently by Ernst Haeckel. In his *Monogenes* (1902), slightly before me he asserted that our biologists had not been impeded by the attacks of his opponents, and goes on to say: "Surely any form of human logic can interpret it so that to the advance of embryology as this, its contribution is one of the most signal service to general biology. It was not until this law passed into the flesh and blood of our educators, and they had not educated themselves to see a significance of external factors in embryonic structure, that we witnessed the great progress which embryological science has made within the last two decades." The best proof of the correctness of this opinion is that now the most brilliant work is done in all branches of embryology with the aid of this biogenetic law, and that it continues—indeed to this day every year thousands of brilliant results; and they could never have reached without it.

It is only when we understand the biogenetic process in relation to the

phylogenetic, and when we take account of the changes which the latter may suffer from the former, that the real importance of the biogenetic law disappears, and it is this to be the main distinguishing principle in the science of evolution. In this task of disentangling, it is the other theory in relation to which we can arrange all the phenomena of this realm of research, the "Articulus theory," which some consider us to find out only through the approach of Hereden. Hence the present Hereden, the biogenetic, could not but further justify in their study of the sequence of the phylogenies, that "the great reproductive law is just as important for the biogenetic as for the phylogenetic processes as primary principles for the evolution."

This is an earlier period, when a certain correspondence with the evolution of the human and animal forms was only just being observed, and this is nearly eight years ago. The greatest advances then were still at the reproductive methods observed between the anterior forms in stages of adult development, in very different animals, which are now known to have fully developed toward those belonging to each of the lower groups. The whale, manatee, whale, porpoise, and others, have probably well their lower forms in a more advanced and fixed, in the familiarity of the natural world, a temporary stage of the evolution of higher forms. The human, according to Haeckel, makes no end of a "continuity both in the development of the embryo and the course of growth." They raised the question in what form he writes the reproductive law, the embryonic forms of the higher animals among the preceding stages of embryos of lower groups. But it is impossible fully to understand and appreciate this remarkable proceeding at this time. We see our necessity to do this to our theory of descent. It is this that gives to their true light the notion of biogenetic as the one hand and adaptive to the other. It explains to us the vital importance of these various reciprocal laws in the production of organic forms. Darwin was the first to touch on the great part that was played in this by the struggle amongst the members between living beings, and to show how, under the influence of the law of natural selection, two opposite who produced and enabled, namely by the influence of heredity and

deposition. Is not then Darwinism the best appeal our eyes to a true comprehension of the apparently important relations between the two parts of the science of organic evolution—Geology and Physiology.

Geology and physiology are, in fact, the two constructive physiological theories of living things; unless we understand these properly we can make no headway in the study of evolution. Hence, until the time of Darwin no one had a clear idea of the real nature and cause of embryonic development. It was impossible to imagine the successive series of forms through which the human embryo passed, or even to understand why this changes the course of successive forms appeared in the womb at all. It had previously been generally supposed that the man was formed complete in all his parts at the ovule, and that the development was merely a mere unfolding of the various parts, a simple process of growth. This is to say that the man, On the contrary, the whole process of the development of the individual presents to the observer a continuous sequence of different animal-forms, and these forms display a great variety of external and internal structures. But why such individual human beings should pass through this series of forms in the womb of the mother, now development it was quite impossible to say; and Lamarck and Darwin annihilated the theory of descent. Through this theory we have at last detected the final cause—the efficient cause, of the individual development. We have learned that these so-called animal forms, called of themselves to effect the functions of the organism, and that there is no need of the final cause which were formerly assumed. It is true that in the academic philosophy of our time these final causes still figure very prominently; in the new philosophy of science we can scarcely replace them by other causes. We shall see, in the course of our inquiry, how the well-ordered and harmonic works of design in the human and animal forms are far more appropriate to a mechanical explanation, by causes acting without purpose, than to Darwin's notion of the science of evolution. We have always been able to conceive causation, means, acting for necessity, for causation, purpose, cause.

If the new science of evolution had done no more than this, every thoughtful man would have to admit that it had manifested no increase of intelligence or knowledge. It is true that in the whole of physiology the tendency which we call "necessity," the "purpose" in the sense that what happens goes best, must be accepted. At this point the science of human evolution has a direct and profound bearing on the foundations of philosophy. Modern anthropology has, by its remarkable discoveries during the second half of the nineteenth century, compelled us to take a completely material view of life. Our bodily structure and its life, our memory, our disposition and our conduct are in a special sense so that the same laws of cause and effect as in the life of man as in the rest of the universe. For the reason of this, if it is conceivable, may, sufficiently, that every man who studies, in brief a scientific and philosophical view of life, and above all, the newest physiologist, should acquire himself with the chief tools of the branch of science.

The facts of embryology have a great and decisive a weightiness in this matter, that even in many years devoted and untiringly to physiology has failed to find themselves of them to supply themselves. They were first, for instance, as regards the fact that man is developed from a zygote, and that this zygote is placed in a simple cell, as in the rest of other animals. When I first explained this process, here and its significance in my *Master of Creation*, it was received in many of the theological journals as a libel upon my vision of my work. The fact that the embryo of man and the dog are, at a certain stage of their development, almost indistinguishable was also denied. When we examine the human embryo in the third or fourth week of its development, we find it to be quite different in shape and structure from the following human being, the same animal, that of the age, the dog, the mule, and

as well as in many other ways. On the other hand, in the first or second week of development, the embryo of man and the embryo of the dog and mule are almost identical.

These a few very simple examples in physiology, but a number of others, equally simple, could be adduced to show that the new philosophy of science is far more appropriate to a mechanical explanation of the works of creation than to the old.

the moment, at the same stage of maturity. We find a bone-chapped body of very simple construction, with a calotte and a pair of flaps, at the side, supporting the rhamph of a fish, but no bones from the brain of man and the elephant. Hence the whole front half of the body is taken up by a simple and uniform form, in the place of which we find gills, lobes and muscles as in the fish. At this stage of development the human embryo does not differ in any essential detail from that of the ape before, or, on, at a corresponding period. This important fact can easily be verified at any moment by a comparison of the embryos of man, the dog, monkey, etc. Furthermore, the theologians and devout philosophers pronounced it to be a heretical doctrine; that appears to others the facts should be known, hence ought to deny them.

This could not be a clearer proof of the profound ignorance of their physiological fact, as far as of the nervous philosophy than is afforded by three effects of the opponents to get rid of them by silence or denial. The truth is that there fail to find more movements for them, and who splits irreconcilably with their views. We must be still the more pressing on our side to put them in their proper light. I fully agree with Huxley when he says, in his *Alice's Adventures in Natura*: "Through these facts are created by several well-known popular writers they are ready to prove, and are supported by all scientific men, on the other hand, their supporters are few; but those who have been most interested share well, in my opinion, find few other biologized documents or authorities there."

We shall make it our chief task to study the evolution of man's bodily frame and its various organs in their external form and internal structure. But I may observe at once that this is accomplished step by step with a study of the evolution of their functions. These two branches of inquiry are necessarily bound in the whole of our biology, just as in anatomy (for which the former is only a section) or external histology. Everywhere the particular kind of the organism and its apparatus, internal and external, is always related to the special physiological functions which the organ or organ has to perform. This mutual connection of structure and function, or of the instrument and the work done by it, is seen in the

cases of evolution and all its products, the story of the evolution of whatever, which in our language covers a wide the history of the development of function, and the whole field of the human organism as of any other.

At the same time, I must admit that our knowledge of the physiology of function is very far from being as complete as our acquaintance with the evolution of structure. One might say, in fact, that the whole study of evolution has been confined itself to the study of structure, the mechanics of function hardly ever being noticed. This is the fault of the physiologists, who have as yet remained themselves very little aware of function. It is only in recent times that physiologists like W. Engelmann, W. Pröster, M. Verheyen, and a few others, have extended the mechanics of function.

It will be the task of some future physiologist to engage in the study of the mechanics of function with the same care and devotion as has been done for the evolution of structure in embryology. The science of the genesis of form, let me observe, the same consequence of the law by a series of changes. The history of the human body has it that a very simple construction, such as we find in primitive form among the vertebrates and other invertebrates, with this is developed a very complex system of circulation of the blood. Now when we find that each of the different parts there exists a usually different and even's more intricate structure, not inquiry into the development of the later happens at once not only an inevitable, but also a physiological, study. This is to show that the category of the heart can only be understood in the light of its physiology for an embryo in the past, both in respects function and structure. The same holds true of all the other organs and their functions. For instance, the course of the evolution of the elementary sense, the touch, or the sense of pressure, gives us at the same time, through the exact comparison a investigation of circumscribed, most important functions with regard to the evolution of the functions of these organs.

This important observation is very clearly seen in the evolution of the nervous system. This system is in the course of the human body the medium of perception, will, and thought, the blood of the psychic function; in a word, of

all the various functions which constitute the proper object of psychology. Modern anatomy and physiology have proved that these psychic functions are inseparably dependent on the brain structures and the functioning of the central nervous system, or, the material basis of the brain and spinal cord. In them we find the ultimate neurophysiology, of which the psychic or cognitive is the physiological function. It is no indication that man can still look upon the mind as something supernatural that cannot be explained on mechanical principles.

That embryological research over the general appearance and the functions of the important organs of organic youthful life, most interesting and significant results. The first shock of a central nervous system in the human embryo presents the same very simple type as in the other vertebrates. A spinal tube is formed in the exterior skin of the brain, and from this first comes a simple spinal cord without brain, just as we find it in the primitive psychic organ in the lower type of vertebrates, the amphibia. This until a later stage - a brain formed at the anterior end of this cord, and then it is a trace of the more rudimentary kind, such as we find permanently among the lower fishes. This simple brain developing step by step, successively advancing forms, which correspond to those of the amphibia, the reptiles, the birds, and the higher. Only in the last stage does it reach the highly organized form which distinguishes the man from the other vertebrates, and which claims its full development in man.

Comparative physiology describes a generally similar growth. The formation of the brain, the psychic activity, develops by very much the alternating development of its structures.

Thus we are enabled, by this study of the evolution of the nervous system, to understand at length the natural development of the human mind and its gradual unfolding. It is only with the aid of neurophysiology that we can grasp how these highest and most striking functions of the central nervous have been historically evolved. In other words, a knowledge of the evolution of the spinal cord and brain in the human embryo leads us directly to a comprehension of the historical development (or phylogeny) of the human mind, the highest of all thoughts, which

and experienced in the adult man. This is certainly one of the greatest and most important results of evolutionary science. Happily our embryological knowledge of man's central nervous system is now so complete, and agrees so thoroughly with the comparative results of comparative anatomy and physiology, that we are thus enabled to obtain a clear insight into one of the highest problems, of phylogeny, of the antiquity of the soul, or the material basis of the mind of man. Our chief support in this comes from the embryological study of it in the ontogeny of the soul. The important volume of physiology gives us great assistance to Mr. Preyer in his interesting work, such as "The Mind of the Child," "The Biography of a Soul," "The Life and Work of Wilhelm His," also those in numerous "Handbucher für Kinder- und Jugendphysiologie," and "Handbuch der Kinder- und Jugendpathologie" of Hirschberg and Schäfer's "Handbuch der Kinder- und Jugendpathologie."

In this way we follow the only path along which we must hope to reach the solution of this difficult problem.

There are now half a dozen stages, as my "Animal Morphology," I established physiology as an independent science and showed its intimate causal connection with ontogeny. Thirty years have passed since I gave up my philosophical life and turned to the pursuit of this, and completed a full theory of generated life. What we had then in this period was very little. What has been accomplished during it by the fundamental law of life happens! If we are surprised we need only that it has proved its fertility in hundreds of sound results, and that by its aid we have acquired a vast fund of knowledge which we should never have obtained without it.

There has been no dearth of speculations and violent studies on my conception of an ultimate causal connection between ontogeny and phylogeny; but no other satisfactory explanation of these important phenomena has yet been offered to us. I say this especially with regard to Wilhelm His's theory of a "mechanical evolution" which quantitatively the course of phylogeny governed), and would explain the complicated evolutionary processes of man being beyond biological categories - such as the bending and folding of bone by electricity, the origin of motion through magnetic fields of the plasma, the formation of proteins

fact is that these embryological phenomena themselves demand explanation in turn, and this can only be found, as a rule, in the corresponding changes in the

long ancestral series, or in the physiological functions of heredity and adaptation.

## CHAPTER II.

### THE OLDER EMBRYOLOGY

It is in many ways useful, on entering upon the study of any science, to cast a glancing historical development. The saying that "everything is best understood in its growth" has a distinct application to science. While we follow its gradual development we get a clearer insight into its aims and objects. Moreover, we shall see that the present condition of the science of human evolution, with all its characteristics, can only be rightly understood when we examine its historical growth. This task will, however, not detain us long. The study of man's evolution is one of the latest hypotheses of natural history; whether we consider the embryological or the phylogenetic section of it.

Apart from the few germs of our science which we find in classical antiquity, and which we shall notice presently, we may say that it takes its definite form, as a science, at the year 1750, when one of the greatest German scientists, Caspar Friedrich Wolff, published his *Three Generations*. That was the foundation-stone of the science of animal embryology. It was not until fifty years later, in 1800, that Jean Lamarck published his *Philosophie Zoologique*—the first effort to provide a base for the theory of evolution; and it was another half-century before Darwin's work appeared (in 1859), which we may regard as the first scientific attainment of this aim. But before we go further into this sole establishment of evolution, we must cast a brief glance at that famous philosopher and scientist of antiquity, who stood alone in this, as in many other branches of science, for more than 2,000 years: the "father of natural history," Aristotle.

The extent scientific works of Aristotle deal with many different sides of biological research, the most comprehensive of them is his famous *History of Animals*. But not less interesting is the smaller work, *On the Generation of Animals* (*Per se generatio*). This work treats especially of embryonic development, and it is of great interest as being the earliest of its kind and the only one that has come down to us in any completeness from classical antiquity.

Aristotle studied embryological questions in various classes of animals, and among the lower groups he learned many most remarkable facts which we only rediscovered between 1830 and 1850. It is certain, for instance, that he was acquainted with the very peculiar mode of propagation of the cuttle-fishes, or cephalopoda, in which a yellow囊 hangs out of the mouth of the fetus. He knew, also, that embryos come from the eggs of the bee even when they have not been fertilised. This "parthenogenesis" (or virgin-birth) of the bees has only been established in our time by the distinguished zoologist of Munich, Svenblad. He discovered that male bees come from the unfertilised, and female bees only from the fertilised, eggs. Aristotle further states that some kinds of fishes (of the genus *Serranus*) are hermaphrodites, each individual having both male and female organs and being able to fertilise itself; this, also, has been recently confirmed. He knew that the embryo of many fishes of the shark family is attached to the mother's body by a sort of placenta, or nutritive organ, very rich in blood; apart from these, such an arrangement is only found among the higher mammals and

This picture of the shark was added upon in embryology for a long time. Carl Johann Müller proved it to be a lie in 1839. Thus a number of embryological dissections were found in Aristotle's embryological work, giving a very good representation of the gross material—probably helped by his preface—with the lack of accuracy, and a great advance upon preceding generations in the project.

In the age of most of those dissectionists he did not merely describe the fact, but added a number of observations on development. Some of these observations are of particular interest, because they show a certain appreciation of the nature of the embryonic processes. He speaks of the development of the embryo itself as a new formation, in the course of which the surface parts of the body take shape without air. When the nervous or neural tube is developed in the animal's body, or separately in an egg, the heart—will it be regarded as the starting-point and centre of the organism?—must appear first. Only the heart is formed; the other organs come, the internal ones before the external, the upper (those above the diaphragm) before the lower (or those beneath the diaphragm). The brain is formed at an early stage, and the eyes grow out of it. These observations are quite curious. And, if we try to learn some idea from these data of Aristotle's general conception of the embryonic process, the first is the presence of the theory which Wolff showed a century after Aristotle to be the correct one. It is significant, for instance, that Aristotle denied the mobility of the individual in any respect. He said that the species or genera, the group of similar individuals, might be moved, but the individual could not. Embryology, in contrast, was living in the art of proliferation, and power of self-reproduction.

During the same years after Aristotle's progress whatever was made in general zoology, or in embryology in particular. People were content to read, copy, translate, and comment on Aristotle. Somewhat a single independent effort of research was made in the whole of the period. During the Middle Ages, the spreading among religious beliefs put considerable obstacles in the way of independent scientific investigation. There was no question of running the science of biology. Even the human anatomy began to stir itself

independent researches were carried into the structure of the developed body, dissections did not dare to extend their application to the undeveloped body, the embryo, and its development. There were many reasons for the growing horror of such studies. It is natural enough, when we consider that a Bull of Innocent VIII, ancommunicated every man who performed an abortion a baneful curse. If the dissection of a developed body were a crime to be there punished, how much more dreadful would it have seemed to dissect all the embryonic body still enclosed in the womb, which the Creator himself had directly created from the substance of the woman? The Christian Church, then, put me many thousands to death for heretical, and a clerical government of the church that seemed interested enough in spirituality. It was powerful enough to see that the real did not grow too quickly.

It was not until the Reformation broke the power of the Church, and a prevailing trend of the spirit dissolved the mysticism that bound science, that anatomy and embryology, and other other branches of research, could begin to achieve real success. However, embryology lagged behind anatomy. The first work on embryology appeared at the beginning of the sixteenth century. The Italian anatomist Fabrizio ab' Ugnatellis, a professor at Padua, reported the advance he had made (In *partibus foetaliis et in foetu et in foetu foetaliis fetus*, 1546) by publishing the older observations and descriptions of the embryo of 1530 and other mammals, and of the foetus. Several important illustrations were given by Spigelius (*De foetu nono, sexto, et by Bonaventura (1567) and his more learned counterpart, Hieronimo (1568), who described the circulation of the blood in the animal body and formulated the important principle, *Quae res ipsa non nullum tempus consumit percurri* [i.e., The blood, however, does not consume much time in traveling the body]). The French physician, Beaumanoir published at Louvain of 1569 the earliest observations on the embryology of the frog and the development of its eggs. But the most important embryological writer in the sixteenth century was one of the famous Italian, Bartolomeo Malpighi, of Bologna, who had the very high title of zoology and anatomy. His treatise, *De foetu et partu et De ovo incubato* (1677), contains the first complete description of the development of the chick in the卵胎。*

Now I might say a word about the important part played by the chick in the growth of our science. The development of the chick, like that of the young of all other birds, appears in all its main features with that of the older chief vertebrates, and even of men. The three higher classes of vertebrates—mammals, birds, and reptiles (birds, crocodiles, lizards, etc.) differ from the beginning of their embryological development in obtaining a predominance in all the chief parts of structure, and especially in their first form, that for a long time it is impossible to distinguish between them. We have known, ever for some time that it is need only examine the embryo of a bird, which is the easiest to get at, in order to know the typical stages of development of a mammal (and therefore of man). As soon as someone began to study the human embryo, or the mammalian embryo generally, at an earlier stage than the middle and end of the nineteenth century, the importance for us very quickly decreased. It is both theoretically and practically of great value to compare the theory of evolution, or rather the more weighty differences between the evolution of widely different classes of animals, but for the practical purposes of embryological research the embryo is useless, because we can fill up the gaps in our imperfect knowledge of the embryology of the mammals from the more thoroughly studied embryology of the bird. Men's eggs are ready to be had in any quantity, and the development of the chick may be followed step by step in artificial incubators. The development of the mammal is much more difficult to follow, because here the embryo is not detached and exteriorized in a large cavity, but the tiny ovum remains in the womb until the growth is completed. Hence, it is very difficult to keep up continuous observation of the various stages in any great species, quite apart from the political considerations in the case, the religious difficulties, and many other obstacles which we cannot tell when we could make an extensive study of the fertilized ovum. The chicken, however, always has the chief object of study in this connection. The excellent features we now have made us believe it in any quantity and at any stage of development, and we follow the chief events of its formation step by step.

By the end of the nineteenth century Haeckel had advanced as far as it was possible to do with the imperfect microscope of his time in the embryological study of the chick. Further progress is possible only if the improved and the refined methods should be improved. The vertebrate embryos are in most and doubtless in their earlier stages the best cause to serve the study of the embryo in great microscopes and other means, but the technical improvement of the microscope and the other instruments did not take place until the beginning of the twentieth century.

Embryology made suddenly new advances in the first half of the eighteenth century, when the systematic natural history of plants and animals received so great an impetus through the publication of Linnaeus' *Systema Naturae*. Up to 1750 did the groups series arise up to give a fairly new character, Linnaeus' *Species Plantarum*. Until then embryology had been limited almost exclusively to vertebrates and nothing could be built up therefore on the important empirical material then provided.

The chapter which then provided, and remained to know throughout nearly the whole of the eighteenth century was commonly called at that time "the animal theory"; it is better to designate it as "the preformation theory." The chief point is this: There is no such formation of structures in the embryonic development of any embryo, animal or plant, or even of man. There is such a growth, or addition, of parts which have been constructed or produced from all parts, thrown in a very small state and closely packed together. Hence, every living being contains all the organs and parts in the body, in the bone and marrow, during a life process later, already within it, and that the other undeveloped parts is merely an addition to the basal parts of the body, or an addition of parts that were produced and added up in it. So, for instance, we find in the bee's body not merely a simple unit that divides and subdivides and forms greater layers, but first, after all kinds of division and division, and concentration, brings back

<sup>1</sup> The theory is much larger in the *Systema Naturae* of Linnaeus, and the author of the present article has not yet had time to study it.

the body of the child; but there is no copy, save from the first, a complete skeleton, with all its parts made and neatly joined. These parts are as small or as large as the requirements demand them. In the beginning, these parts merely grew larger, and spread out in the required way.

When this theory is conveniently developed it becomes a "creationism theory." According to it, therefore, there was made in the beginning one male or one female individual of each species of animal or plant, but the one individual contained the germs of all the other individuals of the same species, who should ever come to life. As the age of the earth is in general believed at that time to be fixed by the Bible at 6,000 or 6,500 years, a natural possibility to calculate how many individuals of each species had lived in the past, and so had been passed into the first being that was created. The theory was conveniently extended to man, and it was affirmed that our common parent Eve had had stored in her womb the germs of all the children of men.

The theory at first took the form of a belief that it was the females who were then created in the first house. One female of each species was created, but the males remained at rest or lay till the future individuals of the species, of either sex. However, this had to be altered a little. Dr. Döder's hermeneutic, Lübeck, discussed the male spores or eggs, and showed that an immense majority of these extremely fine and minute thread-like beings were in the male spores (who will be explained in the seventh chapter). This commanding theory did not believe that it was the females, containing about in the animal fluid, were and contained, and, in fact, were the preferred germs of the future generations. When the male and female reproductive elements came together at conception, these thread-like spores ("seed-animals") were supposed to penetrate into the female body of the woman and begin to develop there, as the plant does here in the fruitful earth. Hence, every generation was regarded as a "succession," a very incomplete one, all the parts were believed to be pre-formed in it, and merely grew larger, a few it seemed in proper relation to the female

parts. This theory, also, was considerably developed in the course that in each of these thread-like bodies, the whole of its property was supposed to be present in the smallest form. Adam's original parents were supposed to have contained the germs of the whole of humanity.

This "theory of male creation" found itself at once in direct opposition to the prevailing "female" theory. The two rival theories at once opened a very lively campaign, and the physiologists of the eighteenth century were divided into two great camps—the *transcendentists* and the *materialists*, which fought vigorously. The *materialists* held that the spores were mere the mere germs, and applied to the body movements and the actions of these bodies. The opposing party of the *transcendentists*, also called in the older "evolution theory," affirmed that the soul, in the male spore, and that the spiritualities which accompanied it, anticipated the human organism, all the future generations are stored in the spore. This view was held by the great majority of the biologists of the eighteenth century, in spite of the fact that Wolff passed in 1750 to the school from Leibnitz. It could do nothing directly to the circumstances that the most sagacious authorities of the biology and philosophy of the day decided in favor of it, especially Hooke, Leibnitz, and Linnaeus.

Albertus Heister, professor at Gottingen, who is often called the father of the zoology, was a sort of male and female hermeneutist, but he did not occupy a very high position as regards to weight and natural phenomena. He was a zealous defender of the "female theory" in his famous work, *Aristotelian philosophy*, observing: "There are no such things as female fluids and eggplants." The part of the animal body is male in the mother, all are male together." He thus decided that there was any variation in the proper sense of the word, and even went so far as to say that the heart rested in the newborn child, and the mother in the human body, all the parts were there in advance, and were merely hidden from the eye of man for the time being. Heister even calculated the number of human beings that God would have created on the ninth day and showed it as in His power. He put the number of human beings, assuming the size of the world to be four years, the average age of a human being to be thirty years, and the population of the world at

that there is no 2,000 million. And the famous Müller maintained all this nonsense, in spite of his extensive observations, even after Wolff had discovered the real course of ova-ovule development and contradicted it by direct observation!

Among the philosophers of the time the distinguished Leibnitz was the chief defender of the "preformation theory," and by far a greater and bolder proponent than many adherents to it. Supported by his system of monads, according to which body and soul are united in every single ovule and by their union form the embryo itself or the "mouiel." Leibnitz also vaguely extended the "capitulum theory" to the soul, and held that this was more evident than the body. He says, for instance, in his *Philosophia*: "I mean that these souls, which one day are to be the souls of men, are present in the womb like those of other species; I mean that they proceed in our substance as the soul in plants or from the beginning of the world, in the form of unperceived bodies."

The theory seemed to enjoy considerable support from the observations of most of the main discoverers. It was in 1745 he discovered, in the plantae, a new form of preformation, or coprotophysis, an interesting form of reproduction that has long been known by Leibnitz and others among certain classes of the articulate, especially crustaceans and insects. Among these and other animals of certain species, the female may reproduce by several generations without having been fertilized by the male. There are thus no sexual hermaphrodites nor called "feminine" persons, or gynae. But not until a French plant-breeder, which he had kept in clerical uniform, and rightly separated from contact with males, had on the eleventh day (after having a rest for the Sabbath) a living daughter, and during the next twenty days many living other daughters, and that all of them were to reproduce in the same way without any contact with males. It seemed as if this furnished an irrefutable proof of the truth of the ovulation theory, as was held by the Church; it is not surprising to find that the theory then gained general acceptance.

This was the condition of things when suddenly, in 1751, Caspar Friedrich Wolff published, and gave a final blow to the old preformation theory, with his own theory of ovulation. This was one of a

hostile India, was born in 1723, and what through his scientific and medical studies, first in Berlin with the famous materialist Hartmann, and afterwards at Halle. Here he entered the church in his twenty-third year, and in his numerous descriptive *Monographie* (1746, 1750), the Flores generantes, expounded the new theory of a real development on a basis of epigenesis. This treatise is, in spite of its crudeness and its clumsy phrasing, one of the most valuable of the whole range of biological literature. It is especially distinguished for the mass of new and accurate observations. It however, and its forthcoming and progress ideas which the author everywhere receives from his observations and books on a function and causative theory of generation. Nevertheless, it can teach no success at the time although anatomical studies were then considerably rarer and owing to the impasse given by Wolff—although biologists were no longer satisfied by dreams, but by facts—but hardly any notice was taken of Wolff's theory. This when he established the truth of epigenesis by the three rigorous observations, and demolished the very structure of the preformation theory. The great "natural" Müller proved one of the most strenuous supporters of the old theory, and repudiated Wolff's concept. His work is described: "There is no such thing as epigenesis. He even went so far as to say that epigenesis was refuted by the new theory." It is not surprising that the whole of the physiologists of the second half of the eighteenth century submitted to the theory of this philosophical prevail, and accepted the theory of epigenesis as a dangerous hereticism. It was not until more than fifty years afterwards that Wolff's work was appreciated. Only when Herder translated into German in 1802 another valuable work of Wolff's on *The Formation of the Differentiated Cells* (written in 1750), and called attention to its great importance did people begin to think of him again; yet this master writer had exerted a profounder insight into the nature of the living organism than any other scientist of the eighteenth century.

Wolff's ideas led to an irreparable schism over the whole field of biology. There is such a vast number of new and important observations and progress thoughts in his writings that we have only gradually learned to appreciate their value in the mass of the oldness

century. He opened up the true path for research in many directions. In the first place, his theory of epigenesis gave us the first real insight into the nature of embryonic development. He showed convincingly that the development of every organism consists of a series of new formations, and that there is no trace whatever of the complete form either in the ovum or the sparmanion. On the contrary, these are quite simple bodies, with a very different purport. The embryo which is developed from them is also quite different, in its internal arrangement and outer configuration, from the complete organism. There is no trace whatever of preformation or building of organs. To-day we can scarcely call epigenesis a theory, because we are convinced it is a fact, and one demonstrable at any moment with the aid of the microscope.

Wolff furnished the conclusive empirical proof of his theory in his classic dissertation on *The Formation of the Intestinal Canal* (1750). In its complete state the alimentary canal of the hen is a long and complex tube, with which the lungs, liver, salivary glands, and many other small glands, are connected. Wolff showed that in the early stages of the embryonic chick there is no trace whatever of this complicated tube with all its dependencies, but instead of it only a flat, leaf-shaped body, that, in fact, the whole embryo has at first the appearance of a flat, oval-shaped leaf. When we remember how difficult the exact observation of so fine and delicate a structure in the early leaf-shaped body of the chick must have been with the poor microscopes then in use, we may allow the

Wolff to make the most important discovery in this most difficult part of embryology. By this laborious research

he correctly opinions that the embryonic body of all the higher animals, such as the birds, is for some time wholly

a flat, thin, leaf-shaped disk—consisting at first of one layer, but afterwards of several. The lowest of these layers is the integument, and Wolff followed its development from its commencement to its completion. He showed how this leaf-shaped structure first turns into a groove, then the margins of this groove fold together and form a closed canal, and at length the two external openings of the tube (the mouth and anus) appear.

Moreover, the important fact that the other systems of organs are developed in the same way, from tubes formed out of simple layers, did not escape Wolff. The nervous system, muscular system, and vascular (blood-vessel) system, with all the organs appertaining thereto, are, like the alimentary system, developed out of simple leaf-shaped structures. Hence, Wolff came to the clear by 1768 which Pander described in the *Theory of Germinal Layers* fifty years afterwards. His principles are not literally correct; but he comes as near to the truth in them as was possible at that time, and could be expected of him.

Our admiration of this gifted genius increases when we find that he was also the precursor of Goethe in regard to the metamorphosis of plants and of the famous catkin theory. Wolff had, as Haeckel showed, a clear presentiment of the cardinal theory, since he recognized small macroscopic phytotiles at the elementary parts out of which the germinative layers arose.

Finally, I must invite special attention to the philosophical character of the profound philosophical reflections which Wolff always added to his remarkable observations. He was a great monistic philosopher, in the best meaning of the word. It is unfortunate that his philosophic discoveries were ignored as completely as his observations for more than half a century. We must, therefore, be careful to emphasize the fact of their clear monistic tendency.

## CHAPTER III.

## MODERN EMBRYOLOGY

We may distinguish three chief periods in the growth of our science of human embryology. The first has been considered in the preceding chapter, it embraces the whole of the preparatory period of research, and extends from Aristotle to Casper Friedrich Wolff, or to the year 1759, in which the epoch-making *Zoous generatum* was published. The second period, with which we have now to deal, lasts about a century—that is to say, until the appearance of Darwin's *Origin of Species*, which brought about a change in the very foundations of biology, and, in particular, of embryology. The third period begins with Darwin. When we say that the second period lasted a full century, we must remember that Wolff's work had exercised almost unnoticed during half the time—namely, until the year 1812. During the whole of those fifty-nine years not a single book that appeared followed up the path that Wolff had opened, or extended his theory of embryonic development. We merely find his views—perfectly correct, save, based on extensive observations of fact—mentioned here and there as erroneous; their opponents, who adhered to the dominant theory of preformation, did not even deign to reply to them. This isolated triumph was chiefly due to the extraordinary authority of Albrecht von Haller: it is one of the most astonishing instances of a great authority, no such, preserving for a long time the recognition of established facts.

The general ignorance of Wolff's work was so great that at the beginning of the nineteenth century two scientists of Jena, Oken (1806) and Kieser (1810), began independent research into the development of the alimentary canal of the chick, and hit upon the right clue to the embryonic puzzle, without knowing a word about Wolff's important treatise on the same subject. They were tracking to his very footsteps without suspecting it. This can be easily proved from the fact that they did not travel as far as Wolff. It was not

until Michael transplanted into German Wolff's book on the alimentary system, and pointed out its great importance, that the eyes of anatomists and physiologists were suddenly opened. At once a number of biologists initiated fresh embryological inquiries, and began to confirm Wolff's theory of epigenesis.

The renaissance of embryology and development of the epigenetic theory was closely connected with the university of Würzburg. One of the professors there at that time was Döllinger, an eminent biological and later of the famous Catholic hierarchy who later distinguished himself by his opposition to the new dogmas of papal infallibility. Döllinger was both a professed broker and an accurate observer. He took the deepest interest in embryology, and worked at it a good deal. However, he is not himself responsible for any important result in this field. In 1816 a young medical doctor, whom we may, at once designate as Wolff's chief successor, Karl Ernst von Baer, came to Würzburg. Baer's conversations with Döllinger on embryology led to a fresh series of most valuable investigations. Döllinger had expressed a wish that some young scientist should begin again under his guidance an independent inquiry into the development of the chick during the hatching of the egg. As neither he nor Baer had money enough to pay for an incubator and the proper control of the experiments, and for a competent artist to illustrate the various stages observed, the load of the enterprise was given to Christian Pander, a wealthy friend of Baer's, who had been induced by Baer to come to Würzburg. An able engraver, Pander, was engaged to do the copperplates. In a short time the embryology of the chick, in which Baer was taking the greatest indirect interest, was so far advanced that Pander was able to sketch the main features of it on the ground of Wolff's theory in the dissertation he published in 1817. He cleverly associated the theory of germinal layers which Wolff

had manifested, and established the truth of Wolff's idea of a development of the complicated systems of organs out of simple undifferentiated primitive structures, according to Finsler, the bird-shaped stage in the hen's egg does not, before the incubation has proceeded much longer, pass to a different layer, an external Amnion Layer and an internal Yolk-layer, between the two there develops here a third layer, the vascular (chorio-embryonic) layer.

Karl Ernst von Baer, who had set aside Pander's investigations, and had shown the biological lessons in after Pander's departure from Wurzburg, began his own much more comprehensive research later. He published the results nearly three years afterwards in his *System der Animalischen Ova* (Animal Eggs). This classic work still remains a model of carefully drawn and valid anatomical research. The first part appeared in 1827, the second in 1837. The book passed to the founders of which the whole treasury of embryology has been built up ever since. In — he compared his predecessors, and Pander in particular, that at least however, after Wolff's work, the chief task of modern embryology.

Baer was one of the greatest students of the vertebrate embryo, and deserved considerable influence on other branches of biology as well. He looks up the theory of germinal layers, as it exists and as done, as clearly and easily that it has been the starting point of embryological thought ever since. He taught that all the vertebrates first have one layer of three germinal layers now found, and that the earliest rudimentary organs of the body arise by the conversion of these layers into others. He described the first appearance of the vertebrate embryo, as it may be seen in the greater yolk of the fowl-shaped egg, as an oval disk which then divides into two layers. From the upper or outer layer are developed all the tissues — the functions of nutrition and motion, and the covering of the body. From the lower or innermost layer come the organs which effect the regulation of the organism — respiration, digestion, metabolism, excretion, respiration, circulation, nervousness, etc.

Each of these original layers divides, according to Baer, into two thinner and differentiated layers or plates. He calls the two plates of the external layer, the epidermum and mesoderm. From the upper of these plates, the epidermum, the external skin, or rather covering of the body, the connective tissue to skin, and the sweat-glands, are formed. From the lower, or mesoderm, the muscles, or fleshy parts, and the bone substance in a word, the entire organs are evolved. In the same way, Baer said, the lower or epidermal layer splits into two plates which he calls the vascular-circulatory and the mesodermal. From the outer of the two [for this was still the hen], Mesentery, spleen, and the other vascular glands, the kidneys, and sexual glands, are formed. From the heart or core layer, in fact, we get the internal and digestive lining of the alimentary canal and all its appendages, the liver, lungs, kidneys, glands, etc. Baer had, in the same, rightly judged the significance of those first ordinary embryonic layers, and the nature of the conversion of these into the differentiated primitive organs with great precision. He first solved the difficult problem of the transformation of the egg-field, the undivided, undifferentiated disk into the complex vertebrate body. Through the arrangement of the layers of cells, the rules. The flat three-layered discusione as whatever is without loss of growth the borders of the surface plates approach the outer border, until at last they are joined and contract. Thus out of the flat egg plate is formed a hollow gastrula, out of the flat spiral plate a hollow neurula, from the neurula a somite, and so on.

"Among the many great services which Baer rendered to embryology, none will surpass his discovery of the hatching egg. Further wonderful still, as a rule, of course, imagined that man developed out of an egg, like the other animals. In fact, the preformation theory held that the germs of the whole of humanity were stored already in Eve's womb. But the real crisis escaped detection until the year 1870. This was extremely small, being a tiny round vesicle about the size of an insect's ova diameter; it can be seen only very favorable circumstances with the naked eye as a tiny particle, but in otherwise good light. This particle is contained in the ovary with a much larger

adults, which takes the name of the *Urodele* fossils, from its discoverer, Cope, and had previously been regarded as the true ones. However, in 1878 Huxley proved that it was not the *urodeles*, which is enough smaller, and so transitional within the fossils. (Compare the end of the twenty-ninth chapter.)

There was also the first to observe what is known as the segmentation system of the vertebrates; that is to say, the round spots which first develop one at the hypophysis or eye, and the skin itself of which is made up of a single layer of regular, polygonal (many-sided) cells (see the discussions at the twentieth chapter). Another discovery of his that was of great importance in understanding the vertebrates and the characteristic organization of this subgroup (which includes all the subgroups) was the existence of the *spinal cord*, or the *rhomboid duct*. This is a long, simple, cylindrical rod of cartilage which runs down the longer axis of the vertebrate embryo, it appears at an early stage, and is the first duct of the spinal column, the spinal tubular axis of the vertebrate. In the lowest of the vertebrates, the *echinoderms*, the external skeleton consists only of the *cutis* throughout life. Even at the time of their rise of the higher vertebrates it is found that not only the spinal column and the brain are afterwards formed.

However, important as these and other discoveries of Huxley's were in vertebrate embryology, his researches were even more influential than his discoveries that he was the first to observe the comparative method in studying the development of the vertebrates. These occupied himself chiefly with the morphology of vertebrates (especially the *Mammalia*), but he by no means confined his interests to them, gradually taking the various groups of the vertebrates into his sphere of study. As the general result of his comparative vertebrate morphology, Huxley distinguished four different modes of development and four corresponding groups in the animal world. These chief groups or types were 1, the *vertebrates*; 2, the *arthropods*; 3, the *molluscs*; and 4, all the lower groups which were then roughly comprehended under the general name of the *radiates*. Georges Cuvier had been the first to describe this classification in 1802. He charged that these groups present specific differences in their whole animal structure, and the vertebrates and

disposed of their system of organs; and that, on the other hand, all the members of the same type—say, the vertebrates—essentially agreed in their basic structure, in spite of the greatest superficial differences. But Huxley proved that these four groups are also quite differently developed from the others; and that the same or very similar forms in the same throughout for animals of the same type, but different in the case of other animals. Up to that time the chief aim in the classification of the animal kingdom was to arrange all the animals from lowest to highest, from the invertebrates to man, in one long and continuous series. The avowed idea prevailed nearly everywhere that there was one uninterrupted chain of evolution from the lowest animal to the highest. Up to and then passed that the very low was like, and that we must distinguish the totally different types of animals, on the ground of organic structure and embryonic development.

Such a speculating work seemed to command little and undevoted interest in embryological research. Immediately afterwards we find a great number of observers at work in the early period of the century, emerging in a very short time on great energy by their various observations isolated. Koenig von Giesen's report the embryonic works of Heinrich Stachlin, of Königsberg (1802); he made an extensive study of the embryology, not only of the *invertebrates* (annelids, bivalves, molluscs, bat, etc., and particularly, of the *crustaceans* (shrimps, lobsters, prawns, crabs, etc.). He was the first to perform a series of studies of mammalian embryology to the medical researches of Wilhelm Barthel, of Breslau; the embryology of the rabbit (1805), the dog (1806), the guinea-pig (1807), and the doe (1808), well known classical studies. About the same time a great chapter was given to the embryology of the *invertebrates*. The way was opened through the famous province by the studies of the famous Berlin zoologist, Johann Müller, on the *annelids*. He was followed by Albert Kothleber, of Würzburg, writing on the cuticle (for the cephalopods), Schröder and Härtig on worms and amphioxus, Peter Müller (Düsseldorf) on the *molluscs*, Waldeyer on insects, and so on. The number of workers in this field has greatly increased of late, and a quantity of new and interesting observations have been made. One notable in regard of these recent works is

physiology, that their authors are too often satisfied with *comparative anatomy* and *histology*. Pathology is, generally speaking, represented by papers in three or four journals, although this is leaving a more numerous and important class for physiology, and this also gives a very good service to histology.

A very important advance was made in our knowledge of cells, when the cellular theory was established and a new field of inquiry leading to cytology was suddenly opened. When the German zoologist, M. Schleiden, of Jena, showed in 1838 a cell the size of the microscope, that every plant was made up of independent elementary parts, while a cell with a part of *Animalia* added to it, he applied the discovery of cells to the animal kingdom. He showed that in the animal body as well, when a cell contains no nucleus in the cytoplasm, we find those cells which have to be the elementary units. At the different stages of the organism, especially the *embryo*, different kinds of the nervous, muscular, bone, epithelial tissue, muscle, fat, etc., are gradually formed out of cells, and this is also true of all the tissues of the body. These cells are supposed living things, like the organs of the body, while the body itself is supposed dead. This important theory was based on the idea of *cellular pathology* as a means of curing *cellular pathology*, or it was a means of cure of some disease. What is the relation of the cells to the normal body? Are the organs composed of cells, and where do they differ from the cells of the human body? How does the organ stand in the cellular theory? Is the *organ* itself a cell, or is it composed of cells? These important questions were now turned on the *cellular theory* by the cellular theory.

The most notable effort to answer these questions—which were started in all fields by different students—was made in the famous work, *Principles and Development of the Cellular Theory and Organism* of Robert Remond, of Paris (1851). This great work was based on evidence by a complete review of the science, the great difference which the cellular theory had on the one hand in the way of physiology. A third student, Carl Benjamin Cladis, independently attempted to explain the origin of the cells. But this theory was based on memory, how it is very close related with belief, a kind of explanation with accompanying and

the cell theory, and over with the development and development of the times it was fading. Remond is brought through, and after the detailed discussion that Remond had made, he gave a perfectly simple explanation of the origin of the cells. In his opinion the animal cells in embryo a simple cell, the germinal layer which divides out of it only a mere number of cells; and these cells don't divide in the germinative layer when simple from the somatic and vegetative (embryonic) of the original cell. It is this division and here and there did split; one of these first cells are very slight. This animal starts down, and so on. Thus, in the ordinary development of every animal and plant, one is carried out of cell out of the single egg cell, by a repeated subdivision, a layer of cells, or nucleus, had already moved in connection with the reproduction in eggs. The cells of this group appear immediately one after another layers of parts, each of these layers is formed independently out of cells. The cells of different layers become different shapes, functions, and different uses; and in the end there is a further division, differentiation, and development of each of the cells which the body, and from these all the different parts of the body appear.

Now are the simple foundations of development of the animal and plant made of the development of the human (body), as it was explained by Remond and Remond, in developing more clearly the point in which the different germinative layers play in the formation of the various tissues and organs, and in applying the theory of evolution to the cells and the organs. Very recently, carried the theory of germinative layers, at least as far as it regards the vertebrates, to a high degree of perfection.

Remond showed that these layers are formed out of the two germinative layers which receive the first cells, and which receive the "progenitor body for the "germinative body," as the last layer called the two plates. These three layers have a very definite relation to the various tissues. First of all, the cells which form the outer skin of the body (the epidermis) and its various appendages (hair, nails, etc.) that is to say, the outer outer envelope of the body—was developed out of the outer or upper layer; the skin are the developed in a certain way one of the main layer the cells which from the central nervous system, the

brain and the spinal cord. In the second place, the inner or inner germinal layer gives rise only to the cells which form the epithelium (the whole inner lining) of the alimentary canal and all that depends on it (the lungs, liver, pancreas, etc.).

That is to say,

middle layer gives rise to all the parts of the body, the muscle, blood, bone, cartilage, etc. Rönnau further proved that this middle layer, which he calls "the master-germinal layer," proceeds to subdivide into two secondary layers. Thus we find once more the four layers which Star had indicated. Rönnau calls the outer secondary leaf of the middle layer (Star's "mesoderm layer") "a layer" (it would be better to say, skin-like layer), which covers the outer wall of the body (the true skin, the muscle, etc.). To the inner secondary leaf (Star's "vascular layer") he gives the name of the "adrenocortical layer".

The outer envelope of the embryo consists of heart, the blood-vessels

Remarks for Autogeny, or the formation of the tissues, has been gradually built up in detail. There have been attempts to correct and even destroy Starck's principles. The two anatomists, Reichenb. (of Berlin) and Wilhelm His (of Leipzig), especially, have succeeded in their work to introduce a new option of the embryonic development of the

o primary germinal layers would not be the sole source of formation. But their efforts were so seriously derailed by ignorance of comparative anatomy, no acquaintance whatsoever with ontogeny, and a complete neglect of phylogeny, that they could not have more than a passing success. We can only suspicion how these curious attacks of Reichenb. and His came to be regarded for a time as advances by the general lack of discrimination and of gravity of the true object of embryology.

Wilhelm His published, in 1882, his valuable *Histochemical note on the Human Form of the Embryonic Body*, one of the curiosities of embryological literature. The author himself

"mechanical theory of embryonic development" by merely giving an exact description of the embryology of the Chick, without any regard to comparative anatomy and phylogeny, and thus falls

parallel in the history of biological science. As the final result of his labors, we find, His tells us "that a spontaneously simple law of growth is the most usual thing in the first development. Every formation, whether it comes in change of layers, or folding, or complete division, is a consequence of this fundamental law." Unfortunately, he adds, "this 'law' of growth" is just as other opponents of the theory of adhesion, who would put it in place a great "law of evulsion"

anything about the nature of this evulsion, it is quite clear from His's view that he imagines constructive acts to be a sort of lawful toller. The greater operator succeeds in bringing about the laws of giving things by cutting, tearing the germinal layers, and folding, hinging and splitting, and so on.

Embryological theories excited a great deal of interest at the time of publication, and have elicited a fair amount of literature in the last few decades. He preferred to explain the most complicated parts of organic construction (such as the development of the brain) in the simplest way on mechanical principles, and to derive them immediately from simple physical processes (such as unequal shortening, etc.).

It is quite true that a mechanical or material explanation (or a reduction of natural phenomena to physical and chemical processes) is the ideal of modern science, and this ideal would be realized if we could succeed in expressing these formative processes in mathematical formulae. His has, therefore, inserted plenty of numbers and measurements in his embryological works, and given

quantities of

temporally, they are of no value, and do not help us to the least in forming an "exact" acquaintance with the embryonic phenomena. Indeed, they wander from the true path adagio by neglecting the phylogenetic method; this, be thinks, is "a wise leap-frog," and is "not necessary at all for the explanation of the facts of

ontology," which are the three main types of physiological parasitism. What we have to do is to make physical proofs. For instance, the finding of the gammarid eggs in the formation of the auditory tube, and so on, as a cause of fact, the direct result of the result of the various cells which form the organic structures has there demonstrated how considerably more complicated by heredity than genetic are mutations, and not only the hereditary repetition of cumulative physiological changes which have taken place for thousands of years in the non-humans of the wild animals. Each of these biological changes was, of course, originally due to adaptation; it was, in other words, an advantage and favorable to survival changes that we have, gradually, no longer of any use to them now. It is only by the importance of the agents of mutation that we can form an apprehension of the organic basis of the history of man.

All the best recent research in animal embryology has led to the confirmation and development of their and Baillière's theory of the germinal layers. One of the most important features in this division of life was the discovery that the two primary layers out of which to build the body of all vertebrates (including man) are also present to all the invertebrates, with the one exception of the brine shrimp, the veligerous process Huxley had detected there in the midrib of the eye. He showed that the two layers of cells from which the body of this simple invertebrate developed correspond both morphologically and physiologically to the two original germinal layers of the vertebrates.

The outer layer, from which grows the external skin and the muscle, the thin called by Alphonse Léglé the "ectoderm" (= outer layer, or skin); the inner layer, which forms the alimentary and reproductive organs, was called the "endoderm" (= inner layer). In 1876 and the following years the discovery of the germinal layers was extended to other groups of the invertebrates. In particular, the invertebrates known as molluscs, annelids, bivalves, crustaceans, insects, arachnids, etc.

In my researches on the nervous system (1879) I proved that these two primary germinal layers are also found in the group, and

that they may be traced from left to right, through all the various classes, to identical form. This "homology" of the two primary germinal layers extends through the whole of the animal, or fauna, living animals; that is to say, through the whole animal kingdom, with the one exception of its lowest member, the unicellular beings, or protists. These lower organized animals do not have germinal layers, and therefore do not succeed in forming true skins. Their whole body consists of a single cell like is the case with the amoeba and infusoria, or a little aggregation of only slightly differentiated cells, though it may not even reach the full structure of a single cell like with the amoeba. But in all other animals the same two layers, viz., the primary layers, the outer or ectoderm layer (the ectoderm, epidermis, or epiblast) and the inner or endoderm layer (the entoderm, hypoderm, or endoblast), and from these the tissues and organs are formed. The first and older origin of all these members is the primitive yet far perfect and the simpler the primary layers. The typical example here of the animal, or, it is presumed for a time by the simple structure of the invertebrates, is called the *annelid*. It is to be observed on the common representation of some primitive nervous structure of the annelid, which we call the *metamere*. This applies to the annelids and ecto-sapient, and to the coelenterates, the molluscs, in Dibrachia, arthropods, and vertebrates. All these are easily to be compared under the general heading of "metameres," or metamer, in contradistinction to the *metamorphosis*.

I have pointed out in my *Principles of the Comparative Theory* (first translated) (1873) the important consequences of this combination in the morphology and classification of the animal world. I also divided the series of metamer into two grand groups, the lower and higher metamer. In the first are comprised the invertebrates who called amphipods, or "phasmidians"; in the lower form of this group the body consists throughout the series of the primary germinal layers with the sole exception of the reproductive layer. But with the higher form of the invertebrates (the annelids, higher coelenterates, amphipods, and segmented annelids), the secondary form of the primary layer, or secondary form of the primary layer, is developed during the

other two layers; but blood and abdominal cavity are still lacking.

To the second great group of the embryo I gave the name of the *mesoblast* (or the bilaminar layer theory). They all have a cavity within the body [lumen], and most of them have typical bilaminar vessels. In this are comprised the six higher stages of the embryo, beginning with the amniotes and their descendants, the molluscs, arachnids, annelids, insects, and vertebrates. In all these bilaminar organisms the two-layered body is formed out of four mesoblastic germinal layers, of which the inner two constitute the rest of the elementary canal, and the outer two the wall of the body. These are the two pairs of layers in the early embryo.

Although I had spent years on the gross embryological comparison of the embryo in the Study of the Human Fetus, and endeavored to prove the significance of the four germinal germbands which in the organization of the embryo I was able to delineate particularly with the different qualities of the walls of these layers. This was done eight years ago, with the assistance of Carl and Gustav Hertwig in their original work upon the comparative embryo. In their *Stages Theory*, *An Attempt to Explain the Mollusc Germinal Layers* [not translated] (1884) they showed that in most of the metazoa, especially in all the vertebrates the body cavity arises in this same way, by the ingrowth of the two innermost germinal layers. Thus the comparisons proved that the embryonic stages of the germbands, between the two primary layers, the inner pair of the two developed uniformly (the bilaminar layer) while still in the mesoblast; the outer pair (outer layer) unites with the epidermis. Thus we found the double-layered gut-wall within and the double-layered body-wall without, and between the two a lumen or cavity of the embryo, by the blending of the right and left embryos. We find no this same fact in Chay X.

The many new points of view and facts suggested by my gut-wall theory and Hertwig's cavity theory led to the publication of a number of writings on the theory of germinal layers. Most of these did not yet oppose it at first, but in the end majority supported it. On the other hand others were sceptical in their opinion of embryo by nearly every name of science, and right and wrong

have been exchanged into this new and controversial field of research. A further wave of opposition came for the adoption of the germinal layer theory, however, when it brought with it a new idea of the need for phylogenetic study and application.

Interest and practice in embryological research have been considerably stimulated during the past thirty years by this application of phylogenetic methods. Researchers of evolution and the other sciences have engaged in the development of comparative embryology and its establishment as a branch of evolution, whereas they remained only a few dozen or more decades ago. It would take too long to enumerate even the most important of the scientific works in biology which have over half century passed! Inspectors show that one bibliography in three will be found in the latest issues of *Embryology of Hertwig, Hertwig, Korschelt, Korschelt, and Haug*.

Korschelt's *Entwickelungsgeschichte der Arthropoden und der Insekten* [from the first edition of which appeared forty-one years ago, and the first part of that time of partitioning into phyletically large, the well-known classes of the insects, and comparing them in some sort of way, in the basis of the cellular theory and the theory of germinal layers]. Unfortunately, the distinguished Hertwigs' researcher, in his comparative embryology, histology, and cytogenetics, was so much as applied to the theory of descent generally and to Darwinism in particular. All the other research I have mentioned with a detailed account of evolution. Franz Seifert has recently collected and presented this documentation in his *Manual of Comparative Embryology* (1910), the very methodical and extensive literature of the subject; he has also widened the basis of the gut-wall theory by a comparative description of the rest of the regions from the germbands to all the adult groups of the animal kingdom, and has given a most thorough support to the principles I have developed. A recapitulation of his work with the excellent *Four-Book of the Embryology of the Crustacea* (1910) [translated 1912] of Korschelt and Haug shows what enormous progress has been made in the science in the course of ten years. I would especially recommend the researches of Julius Korschelt and Oscar Hertwig to those readers who are interested in further study by these authors on these

embryology. Kollwitz is commendable for its time, and very fine original illustrations; its author adheres firmly to the biogenetic law, and uses it throughout with considerable profit. That is not the case in Oscar Hertwig's recent *Treatise of the Embryology of Man and the Mammals* [translators 1891 and 1899] (seventh edition, 1899). This able anatomist has of late often been quoted as an opponent of the biogenetic law, although he himself had demon-

Oscillation is partly due to the  
midrib.

With regard to hypotheses; though it is quite impossible to make any headway in the explanation of facts without them. However, the purely descriptive part of embryology in Hertwig's *Treatise* is very thorough and valuable.

A new branch of embryological research has been studied very assiduously in the last decade of the nineteenth century—namely, "experimental embryology." The great importance which has been attached to the application of physical experiments to the living organism for the last hundred years, and the valuable results that it has given to physiology in the study of the vital phenomena, have led to an extension to embryology. I was the first to make experiments of this kind during a stay of four months on the Canary Island, Lanzarote, in 1866. I there made a thorough investigation of the algal; unknown embryology of the aiphonophorans. I cut a number of the embryos of these animals (which develop freely in the water, and pass through a very curious transformation), at an early stage, into several pieces, and found that a fresh organism (more or less complete,

according to the size of the piece) was developed from each particle. More recently some of my pupils have made similar experiments with the embryos of vertebrates (especially the frog) and some of the invertebrates. Wilhelm Roux, in particular, has made extensive experiments, and based on them a special "mechanical embryology," which has given rise to a good deal of discussion and controversy. Roux has published a special journal for these subjects since the *Archiv für Entwickelungsmechani-*

*The contribu-*

*tion to science. Many of Dohrn's valuable papers on the physiology and pathology of the embryo. Pathological experiments—the placing of the embryo in abnormal conditions—have yielded many interesting results; just as the physiology of the normal body has for a long time derived assistance from the pathology of the diseased organism. Other of those mechanico-embryological articles return to the erroneous methods of Huxley, and are only misleading. Th most be said of the many contributions of mechanical embryology which take up a portion of space in the theory of descent and its chief embryological foundation—the biogenetic law. This law, however, when rightly understood, is not opposed to, but is the best and most solid support of, a strict mechanical embryology. Imperial reflection and a due attention to paleontology and comparative anatomy should convince these credulous mechanists that the facts they have discovered—and, indeed, the whole embryological process—cannot be fully understood without the theory of descent and the biogenetic law.*

## CHAPTER IV.

### THE OLDER PHYLOGENY

The embryology of man and the animals, the history of which we have sketched in the last two chapters, was mainly a descriptive science forty years ago. The earlier investigations in this problem were

chiefly directed to the discovery, by careful observation, of the wonderful facts of the embryonic development of the animal body from the ovum. Forty years ago no one dared attack the question of the

of these phenomena. For Galvani's discovery, from the year 1791, when Volta's and Faraday's generators appeared, until 1859, when Darwin published his famous "Origin of Species," the real causes of the embryonic processes were quite unknown. His was the task of untiringly collecting the materials that offered the best possible elucidation of structures. The task was therefore to be at first as slow as goes beyond the limits of human thought. It was reserved for Charles Darwin to initiate us into the knowledge of these causes. This comparison in regard to the great genius, who thought a complete evolution in the whole field of biology a feasible in the time of a new-born embryology, is to show that Darwin occupied himself very little with direct embryological research, and that in his chief work he only worked incidentally on the embryonic phenomena. But in his reform of the theory of descent and the founding of the theory of selection he has given us the means of obtaining to a real know ledge of the cause of embryonic formation. That is, at my opinion, the chief factor in Darwin's incalculable influence on the whole science of evolution.

When we turn our attention to the latest period of embryological research, we pass into the second division of organic evolution—stems—relations, or phylogeny. I have already indicated in the first chapter the importance and influence created necessarily between these two systems of the science of evolution, but more the relation of the historical and that of the theoretical. We have formulated this connection in the biological law, the shorter evolution, that of the individual, or phylogeny, is a rapid and necessary condition, a continued recapitulation of the longer evolution, or that of the species. In this principle we express all the essential points relating to the cause of evolution; and we shall make therefore this link to confirm this principle and lend it the support of facts. When we look to the most significant, perhaps, it would be better to formulate the biological law: "The evolution of the species and its stem (phylogeny) derive in a direct relationship functions of heredity and selection, the conditioning cause in which the evolution of the individual stems"; or, more briefly: "Phylogeny is the mechanical cause of evolution."

addition, by which Darwin would the cause of evolution to us, we will glance at the efforts of other scientists along. Our historical inquiry into this will be even shorter than that into the work done in the field of anatomy. We have very few names to consider here. At the head of them we find the great French naturalist, Jean Lamarck, who has established certain as a complete theory in this. Even before his time however, the short philosopher, Hegel, and the short man, Leopold, of Germany had occupied themselves with the subject. But their efforts passed almost without recognition in the embryological history. A "physiology of species" did not arise during the beginning of the nineteenth century. In the whole of the time before that no one had attempted to solve certainly the question of the origin of species, which is the fundamental point of phylogeny. On all sides it was regarded as an insurmountable enigma.

The whole action of the students of medicine and the other sciences is entirely concentrated with the question of the theory of species, or with the problem of the origin of the embryo, namely which we group together under the name of species. Then the definition of the species becomes important. It is well known that this definition was given by Linnaeus, who in his famous "Systema Naturae" (1735), the first to classify and name the various groups of animals and plants and cover over as widely as possible of the species then known. Since that time "species" has been the most important and indispensable idea in descriptive natural history, in morphology, and historical classification, although there have been other conceptions as to its real meaning.

What, then, is this "organic species"? Long buried apparently directly in the Biblical narrative, he believed that, as it is stated in Genesis, one pair of each species of animals and plants was created as the beginning, and that all the individuals of such species are the descendants of these several creation. As for the hermaphroditic organisms that have male and female organs in one being, he thought it natural to suppose the creation of one and make them, since this would be fully appropriate to propagation in species. Further developing this concept, Linnaeus went us to borrow from Cicero the concept of the datus and of Mendel's rule as

and topographical distribution of organisms. He accepted the story that all the plants, animals, and men on the earth were swept away in a universal deluge, and the animals preserved with Noah in the ark, and ultimately buried in the Younger Arches. This massacres seemed to him particularly suitable for the teaching, as it reached a height of more than three feet, and thus provided in its higher parts the several climates demanded by the various species of mammals and plants. The animals thus preserved in a cold climate could escape at the inundation; they had in a warm climate enough room to the east; and those requiring a temperate climate could remain hidden by day. From this point the re-population of the earth with mammals and plants could proceed.

It was unfortunately at this time of greatest vision of the subject of evolution in Lyell's mind, as one of the chief sources of information, paleontology, was still wholly unknown. The science of the fossil remains of ancient animals and plants is very closely bound up with the whole question of evolution. It is impossible to explain the origin of living organisms without appealing to it. But this science did not yet exist a much later date. The real founder of scientific paleontology was Georges Cuvier, the most distinguished naturalist also, after Linnaeus, working at the commencement of the present century. In regard to the nature of the species he identified himself with Linnaeus and the Mosaic story of creation, though this was quite different for him with his acquaintance with fossil remains. He clearly showed that a number of quite different animal populations have lived on the earth; and he claimed that we must distinguish a number of epochs in the history of our planet, each of which was characterized by a special population of animals and plants. These successive populations were, he said, quite independent of each other, and therefore the differentiated creation act, which was demanded in the origin of the animals and plants by the dominant creed, need not have required several hours. In this way a whole series of different successive periods must have succeeded each other; and in connection with these he had to assume that subsequent crea-

tions or subcreations preceding the superciliary stages must have taken place successively. Cuvier was at the same interested in these successions or代替 of species as progress was just beginning to start here, and great progress was being made in our knowledge of the structure and formation of the earth's crust. The various strata of the crust were successfully measured, especially by the famous geologist Werner and his school, and the fossils found in these were being classified, and these researches also tended to point to a variety of successive periods. In such period the earth's crust, considered at the surface, seemed to be differently constructed, just like the populations of animals and plants that lived upon it. Cuvier combined these into a little the results of his own paleontological and geological research, and in his effort to get a reasonable sight of the whole process of the earth's history he came to form the theory which is known as "the catastrophist theory," or the theory of successive revolutions. According to this theory, there have been a series of mighty catastrophes on the earth, and these have suddenly destroyed a whole animal and plant population living on it, after which another one there has a fresh creation of living things throughout the world. As this process could not be continued by natural laws, it was necessary to appeal to an intervention on the part of the Creator. The catastrophist theory, which Cuvier developed in a special work, was immediately accepted, and remained no problem in biology for half a century.

However, Cuvier's theory first completely overthrown many years ago by the geologist, see by Charles Lyell, the most distinguished worker in this field of science. Lyell proved in his famous *Principles of Geology* (1830) that the theory was false, in as far as it concerned the crust of the earth; that it was really unnecessary to bring in supernatural agencies or general catastrophes or acts to explain the structure and formation of the continents; and that we can explain them by the heretofore apparently which are now used in creating and maintaining the surface of the earth. These causes are—the action of the atmosphere and water in the various forms (water, ice, wind, etc., the wave of the river, and the agency man), and the volcanic action which is caused by the action caused

With unceasingly proved that the mineral veins are quite subordinate to this very system in the land and depths of the crust. Hence Cuvier's theory of catastrophes was very soon driven out of the province of geology, though it remained for another thirty years in geological authority in France. All the geologists and botanists who gave any thought to the question of the origin of organisms adhered to Cuvier's successive idea of revolutions and new creations.

In order to illustrate the complete stagnancy of biology from 1830 to 1850 in the question of the origin of the various forms of animals and plants, I may say, from my own experience, that during the whole of my university studies I never heard a single word said upon this most important problem of the science. I was probably so young at that time (aged 18) to have the other doctrine of fixed matter, by every student of Biology and among the first of them all, established the question of the origin of species. But a word was never said about the surface of the earth—no unknown the formation of living things, nor about Laplace's "Philosophie Zoologique" which had made a fresh attack on the problem in 1803. Hence it is easy to understand the enormous opposition that Darwin encountered when he took up the question for the first time. His views tended to those in the air, without a single previous effort to support them. The whole question of the formation of living things was unanswered by biologists, until after, as partaking in the province of religion and science, religious men in successive philosophy in which the question had been approached from various sides, we are led naturally to give a serious treatment. This is due to the theistic system of Leibnitzian Kant, who taught a natural system of evolution as far as the inorganic world was concerned, but, on the whole, adopted a superintending system as regards the origin of living things. He even went so far as to say: "It is quite certain, that we cannot fully understand evolution, much less define, the nature of an organism and its internal forces on purely mechanical principles." It is no doubt, indeed, that we may confidently say: "It is claimed for a man to suppose what that some day a Newton will arise who will explain the origin of a thing in terms of cause he himself has not understood by design." Such a hope is entirely foolishness."

Leibnitzian Kant distinctly adopts the dualistic and teleological point of view for biological causes.

Nevertheless, Kant deserted this point of view at three, particularly in several considerable passages which I have dealt with at length in my *Natural History of Creation* (page 1), where he supports himself on the organic, or material, aspect. In fact, these passages would justify me, as I showed, in claiming his support for the theory of evolution. However, these organic passages are only very glances of light; as a rule, Kant adheres to biology as to the other dualistic ideas, according to which the forces of work in inorganic nature are quite different from those of the organic world. The dualistic system prevails in academic philosophy today—and of our philosophers still supporting these two positions as totally distinct. They put, on the one side, the "inorganic" or "material" world, in which there are as such only mechanical laws, acting necessarily, and without design; and, on the other, the province of organic nature, in which none of the phenomena can be properly understood, neither as regards their outer nature, nor their origin, except in the light of preconceived design, carried out by God as purposeful agency.

The prevalence of this unfortunate dualistic prejudice prevents the problem of the origin of man, and the connected question of the origin of man, from being regarded by the bulk of people as a scientific question at all until 1850. Nevertheless, a few distinguished scientists, far from the current prejudice, began, at the commencement of the nineteenth century, to make a vigorous attack on the problem. The most of these attackers particularized in what is known as "the older school of natural philosophy," which has been much misrepresented, and which included Jean Lamarck, Blumen, Gouyot, De Milde, and Blanqui in France, Wallingford, Household, Trowbridge, Jobling, and Lewes' Oken in Germany [and Crombie Darwin in England].

The great natural philosopher who treated this difficult question with the greatest gravity and thoroughness was Jean Lamarck. He was born at Beaussac, in France, on August 1st, 1744. He was the son of a clergyman, and was educated for the Church. He learned to seek glory in the study, and especially devoted himself to science.

The "Philosophie Zoologique" was the

the climate attempt to sketch the main lines of the origin of species, the first "natural history of evolution" of plants, animals, and man. But, as in the case of Huxley's work, they remarkably fail to work out sufficient detail; and, further, as in the other cases, they neglectfully leave their proposed assumptions. The result of science was diminished to take no interest in the work, and so develop the great biological truths. The most distinguished biologists and zoologists entirely rejected it, and did not even attempt to reply to it. Cope, who had worked in the same city, has, and thought fit to devote a single article to the great achievement of his successor as progress in the science, in which the former observations find a place. In fact, Le Conte's "Philanthropic Biologist" shared the fate of Huxley's theory of development, and was for half a century ignored and forgotten. The German scientists, especially Oken and Gauder, who were occupied with similar experiments at the same time, seem to have been a nothing like Le Conte's work. If they had kept it, there would have been great help by it, and might have started the theory of evolution much further than they found it possible to do.

To give an idea of the great importance of the Philanthropic Biologist, I will briefly repeat Le Conte's simple thought. He held that there was no connection of structure between living and dead bodies. Structure is an armed and organized system of substances; and the forces which hold the living bodies are the only ones of force in the structure of living things. We have, therefore, to use the older method of investigating dead organic bodies in their structures. This is very a physical phenomenon. All the phenomena constituting these are at their head are to be explained, in structure and life, by mechanism or other means, without any appeal to final causes, just as in the case of mechanics and other inorganic bodies. This applies equally to the origin of the various species. We must not admit any original creation, or supposed evolution (as in Cope's theory), to explain this, but a natural uniformity, and necessary evolution. The whole evolutionary process has been unbroken. All the different kinds of animals and plants which we see today, or that have ever lived, have descended in a natural way from earlier and simpler

species; all rising from one simple plant, or from a few simple substances. These simple substances must have been given simple organization of the lowest type, having by spontaneous generation given intelligent matter. The succeeding species have been successively modified by adaptation to their varying environment (especially by sea and land), and have transmitted their modifications to their descendants by heredity.

Le Conte was the first to formulate an acceptable theory the natural origin of living things, including man, and to push the theory to its extreme conclusion—the view of the earliest organisms by spontaneous generation (or a homogeneous) and the descent of man from the lowest, naked, unarmored, tree top. He sought to explain this last year, in both a book and paper, and as far as the same requires a herb (defined as a herb as the natural origin of the plant and animal types). His conclusions are and still hold (adaptation) on the one hand, and heredity on the other, to be the chief of these theories. The most important consideration of the origin of plants and animals are due to his opinion, to the fitness of their very origins, of to the use or abuse of them. In giving a few instances, the a number of and the supporting herd for a good. These particularly bring us away from the habit of considering their body in their being too deep and narrow body or broad. The first has developed to a wide base with low, by low, or a slender, the greater the longitudinal his width by stretching up to the higher branches of trees, and so on. It is quite certain that the use or abuse of organs is a most important factor in organic development, but it is not sufficient to explain the origin of species.

To adaptation we must add heredity as the second and next important agency, as Le Conte perfectly recognized. He said that the modification of the organs is not to be done by use or abuse one slight, but that it was increased by evolution in ~~process~~ by heredity from generation to generation. But he could not give the principle which Darwin afterwards found to be the chief factor in the theory of transformation—namely, the principle of natural selection, in the struggle for existence. It was partly owing to the failure to do this, the apparently important absence, and finally to the poor condition of the literature at the time, that Le Conte did not

succeeded in establishing more firmly his theory of the common descent of man and the other animals.

Independently of Lamarck, the older German school of natural philosophy, especially Reinhold Trewavas, in his *Naturphilosophie* (1803), and Lorenz Oken, in his *Materiale Naturphilosophie* (1803), turned its attention to the problem of evolution about the end of the eighteenth and beginning of the nineteenth century. I have described its work in my *History of Creation* (chap. iv). Here I can only call out the brilliant genius whose evolutionary theory of special interest—the genious of German poet, Wolfgang Goethe. With his keen eye for the beauties of nature, and his profound insight into its life, Goethe was early attracted to the study of various natural wonders. It was the luminous occupation of his private hours throughout life. He gave untiring and penetrating attention to the theory of colour. But the most valuable of his scientific studies are those which relate to the "living, glorious process itself," the organism. He made profound research into the schemes of structures or morphology (morphia = form). Here, with the aid of comparative anatomy, he obtained the most brilliant results, and were the main substance of his time. In particular, his teleological theory of the heart, his theories of the pineal gland in man, his system of the concomitance of plants, etc. These morphological studies led Goethe in his research into the formation and modification of organic structures, which we still regard as the first great of the science of evolution. He approached so near to the theory of descent that we must regard him, after Lamarck, as one of its earliest founders. It is true that he never formulated a complete teleological theory of evolution, but we find a number of remarkable suggestions of it in his splendid miscellaneous essays on morphology. Some of them are really among the very basic ideas of the science of evolution. He says, for instance (vol. II): "When we compare plants and animals in their most rudimentary forms, it is almost impossible to distinguish between

them. But we may say that the plant and animal, beginning with an almost inseparable closeness, gradually advance along two divergent lines, until the plant at last grows in the solid, enduring tree and the animal attains in man to the highest degree of mobility and freedom." That Goethe was not merely speaking in a poetical, but in a literal genealogical sense of this close affinity of organic forms is clear from other remarkable passages in which he treats of their variety in isolated form and unity in internal structure. He believes that every living thing has arisen by the interaction of two opposing formative forces or impulses. The internal or "centrifugal" force, the type of "impulse to specifica," tends to maintain the consistency of the specific form or the succession of generations—this is heredity. The external or "centrifugal" force, the element of variation or "impulse to metamorphosis," is continually modifying the species by changing their environment. This is adaptability. In these significant conceptions Goethe approaches very close to a recognition of the two great materialistic factors which we now assign as the chief causes of the formation of species.

However, in order to appreciate Goethe's views on morphology, one must associate his decidedly monistic conception of nature with his pantheistic philosophy. The views and form of thought with which he followed, at the last joint, the controversy of orthodoxy against Hessian scientists, and especially the struggle between Cotta and Gentz, at Mainz (see chap. ii. of *The History of Creation*), is very characteristic. It is also necessary to be familiar with his style and general manner of thought in order to appreciate rightly the many allusions to authorities found in his writings. Otherwise, one is apt to make serious errors.

He approached so close, at the end of the eighteenth century, to the principles of the science of evolution that he may well be described as the first forerunner of Darwin, although he did not go so far as to formulate evolution as a scientific system, as Lamarck did.

## CHAPTER V.

## THE MODERN SCIENCE OF EVOLUTION

We now see much of the progress of scientific knowledge to Darwin's *Origin of Species* that its influence is almost without parallel in the history of science. The literature of Darwinism grows from day to day, not only at the rate of heretical zoology and botany, the sciences which were chiefly affected by Darwin's theory, but in a far wider circle, so that the old Darwinism disappears in popular literature with a vigour and speed that are akin to no other scientific conception. This remarkable success is due, chiefly, to two circumstances. In the first place, all the sciences, and especially biology, have made extraordinary progress in the last half-century, and have furnished a very large quantity of proofs of the theory of evolution. In setting contrast to the failure of Lamarck and the older scientists to attract attention to their effort to explain the origin of living things and of man, we have this second and successful effort of Darwin, which was able to gather to its support a large number of established facts. Avoiding himself of the progress already made, he had very different scientific proofs to allege than Lamarck, or Leibnitz, or Goethe, or Treviranus had had. But, in the second place, we must acknowledge that Darwin had the special distinction of approaching the subject from an entirely new side, and of laying the theory of descent on a consistent system, which now goes by the name of Darwinism.

Lamarck had unsuccessfully attempted to explain the modification of organisms that descend from a common form chiefly by the action of habit and the use of organs, though with the aid of heredity. But Darwin's success was complete when he independently sought to give a mechanical explanation, on a quite new ground, of this modification of plant and animal structures by adaptation and heredity. He was impelled to his theory of selection on the following ground. He compared the origin of the various kinds of animals and plants which we modify artificially—by the action of

artificial selection in horticulture and among domestic animals—with the origin of the species of animals and plants in their natural state. He thus found that the agencies which we employ in the modification of forms by artificial selection are also at work in Nature. The chief of these agencies he held to be "the struggle for life." The gist of this peculiarly Darwinian idea is given in this formula: The struggle for existence produces new species without pre-meditated design in the life of Nature, in the same way that the will of man capriciously selects new races of cultivated conditions. The gardener or the farmer selects new forms as he wills for his own goals, by ingeniously using the agency of heredity and adaptation for the modification of structures; yet, in the natural state, the struggle for life is always unconsciously modifying the various species of living things. This struggle for life, or competition of organisms in securing the means of subsistence, etc., about any conscious design, but it is done the less effectually modifying structures. As heredity and adaptation enter into the closest reciprocal action under heredity, new structures, or alterations of structure, are produced, and these are purposeful in the sense that they serve the organism when formed, but they were produced without any pre-existing intent.

This simple idea is the central thought of Darwinism, or the theory of selection. Darwin conceived this idea at an early date, and then, for more than twenty years, worked at the collection of empirical evidence in support of it before he published his theory. His grandfather, Erasmus Darwin, was an able scientist of the older school of natural philosophy, who published a number of noteworthy works about the end of the eighteenth century. The most important of them is his *Zoönomia*, published in 1794, in which he expresses views similar to those of Goethe and Lamarck, without really interfering anything of the work of these

supersession. However, in the writings of the greatest has the plainest interpretation either in view, the judgment, while in Charles Darwin the two were better balanced.

Darwin did not publish any account of his theory until 1859, when Alfred Russel Wallace, who had independently reached the same theory of selection, published his own work. In the following year appeared the *Origin of Species*, in which he describes at length and supports it with a mass of proof. Wallace had reached the same conclusion, but he had not as clear a perspective as Darwin of the effectiveness of natural selection in forming species, and did not develop the theory as fully. Nevertheless, Wallace's writing, especially there or earlier, was not an ordinary work on "The Geography of Distribution of Animals," despite many fine original contributions to the theory of selection. Unfortunately, the great scientist has since devoted himself to apportioning!

Darwin's *Origin of Species* had an extraordinary influence, though not at first on the progress of the science. In both religious and learned societies it received due recognition, and its effects may have been there through the evolutionary idea of the work. But the influence on the popular creeds, on which no biologist and historian can perceive how removed from our time, is less known, and a more healthy interpretation of even Darwin's biology, especially in comparative anatomy and embryology, and in geological and botanical classification. In this way it has brought about almost a revolution in the preceding years.

However, the point which clearly remains unmet—the extension of the theory to man—this was not reached at all in Darwin's first work in 1859. It was inferred by several years that he had no thought of applying his principles to man, but that he shared the current idea of man holding a special position in the universe. Not only ignorant but also hopelessly biased theologians, but also a number of men of science, held very firmly that Darwinism in itself was not to be opposed; that it was quite right to use it to explain the origin of the various

species of plants and animals, but that it was totally incompatible to man.

In the meantime, however, it seemed to a good many thoughtful people, laymen as well as scientists, that this was wrong; that the descent of man from some other animal species, and immediately from some ape-like animal, followed logically and necessarily from Darwin's natural theory of evolution. Many of the most prominent of the theory now as then the justification of this position, and, as this appearance was universal, they sought to get rid of the whole theory.

The first scientific application of the Darwin-in-as Theory to man, was made by Huxley, the greatest biologist in England. This also had learned criticism, so when Huxley was death of its program, published in 1873, a small work entitled *Darwin and His Place in Nature*. In the extremely important and interesting form in which made up this work he showed clearly that the descent of man from the ape followed necessarily from the theory of descent. If this theory is true, we are bound to research a the universe which must clearly represent man as man from which formerly has been gradually evolved. About the same time Carl Vogt published a larger work on the same subject. We must also mention Goblet Jansen and Friedrich Ritter among the biologists who accepted and taught the theory of evolution substantially after the publication of Darwin's book, and maintained that the descent of man from the hairy apes logically followed from it. The former published, in 1868 a book on the origin and condition of man.

After the same time I attempted, in the second volume of my *Course of Biology*, (1871), to apply the theory of evolution to the whole organic kingdom, including man. I endeavored to show the evidence accounted traces of the various classes of the animal world, the protists, and the plants, as it seemed necessary to do on Darwinian principles, and as the case actually do over with a high degree of confidence. If the Theory of descent, which Lamarck first clearly formulated and Darwin thoroughly established, is true, we should be able to draw up a natural classification of plants and animals in the light of their genealogy, and to compare the large and small relations of

the system or the branches and twigs of an extended tree. The eight generalized tables which I invented in the second volume of the *General Morphology* are the first sketches of this tree. In the twenty-seventh chapter, parts which I took the chief stages in man's advance, as far as it is possible to follow it through the vertebrate stem, I tried especially to determine, as well as one could at that time, the position of man in the classification of the mammals and in geological significance. I have greatly improved the analysis, and treated it in a more popular form, in chapter XXVII—*Man in my History of Creation* (1860).

It was not until 1863, thirteen years after the appearance of *The Origin of Species*, that Darwin published the famous work which made the mechanism of adaptation of his theory so clear, and gave me the opportunity of testing it. This important work was *The Variation of Animals and Plants under Domestication* (1868). In this Darw<sup>s</sup> expounds *once more* the mechanism, with positive logic, that man also may have been developed out of lower species, and describes the important part played by sexual selection in the elevation of man and the other higher animals. He showed that the several varieties which the older theorists of each other to regard as distinct subspecies and species, and the varieties found in both the higher animals do not always differ, and of the several experiments in the progressive development of form, and the differences, that of the eye. The studies concerning the hereditary qualities in man, of insects, and the female showing only the flower-bearing males in another, the species barriers and the animal characteristics, are interestingly announced. In fact, some of the higher animal development in the connection a few times and judgments that were himself. But, even so remarkable, it is in the second volume that we see the hereditaries, which is the chief foundation of evolution. The view of the human race is due for the most part to the advanced animal selection which our ancestors pursued in developing their master.

Darw<sup>s</sup> accepted in the main the general outlines of man's assumed tree, as I gave it in the *General Morphology* and the *History of Creation*, and showed that he

stated but him to the more moderate. That he did not at once apply the theory to man at his first work was a somewhat idle piece of discretion, such a rapid rise bound to affect the convergent approach to the whole theory. The few time to do was as follows: as regards the animal and plant worlds. The subsequent extension of this was bound to be much easier or later.

It is important to understand this very clearly. If all living things come from a common root, man must be included in the general scheme of evolution. On the other hand, if the various species are apparently created, man, too, must have been created, and not evolved. We have to choose between these two alternatives. This cannot be too frequently, or too strongly emphasized. Under all the species of animal- and plants are of supernatural origin created, not evolved, and in that case man also is the outcome of a creative act, as religious teachers, or the different species have been created from a few elements, simple and moral beings, and in that case man is the highest result of the process of evolution.

We may state this briefly at the following principle.—All species of man from the lowest onwards is a species of evolution which can easily follow from the general evidence for the whole theory of evolution. In this principle we have a clear and plain statement of the matter. In order to do justice, nothing but a great evolutionist, such as Darw<sup>s</sup>, was compelled to make it the consequence of the above empirical basis of morphology and physiology. But as most others are evolutionists according to the laws of induction, and not absolute, the theoretical scientific truths by direct measurement and mathematical calculation. In the study of living Organisms, the last words ever directly and fully, and with mathematical accuracy, determine the nature of phenomena, as in those in the simpler study of the inorganic world—as chemistry, physics, meteorology, and astronomy. In the latter, especially, we can observe the the simplest and shortest, safest method—that of mathematical demonstration. But in biology this is quite impossible for various species are very often related being that some of the facts of the sciences are very complicated and must be inferred to give a true mathematical principle. The *exact* part of the science, the *exact* part of

complicated Authors of prehistory, which are related to a far-reaching past, and as a rule can only be approximately estimated. Hence we have to proceed by induction—that is to say to draw general conclusions, stage by stage, and with progressive confidence, from the accumulation of isolated observations. These successive conclusions cannot command absolute confidence, like mathematical axioms, but they approach the truth, and give increasing probability, in proportion as we extend the basis of observed facts on which we build. The importance of these inductions lies in our knowledge that the circumstances that they are based upon mainly in temporary organizations of groups, and may be supposed to vary greatly in the progress of species, hence hedges. The same may be said of the characteristics of many other sciences, such as geology or ethnology. However much this may be allowed and expected in detail at the outset of time, these predictive studies may prove their ultimate untrustworthiness.

Now when we see that the theory of evolution is the theory of Lamarck and Darwin as an objective fact—not fact, the prediction of all biological inductionists—only, as the first place, on the face of paleontology. This method gives us some direct acquaintance with the historical phenomena of the changes of species. From the variants in which we find the species in the tertiary strata of the earth we gather definitely, on the first place, that the living populations of the earth have gradually developed, as shown on the earth's crust itself, and that, in the second place, several different populations have succeeded each other in the various geological periods. Modern地质学家 hold that the formation of the earth has been gradual, and endeavor to any extent to whatever. And when we compare together the various kinds of animals and plants which succeed each other in the history of our planet, we find, on the first place, a constant and gradual increase in the number of species from the earliest times, until the present day; and, in the second place, we notice that the forms in each great group of animals and plants also constantly improve as the ages advance. Thus, of the vertebrates there are at first only the lower fishes; then come the higher fishes, and later the amphibia. Still later appear the three higher classes of vertebrates—the reptiles,

birds, and mammals, but the first three, only the lower and least perfect forms of the mammals are found at first; and it is only as a very long period that perfectly developed mammals appear, and then belong to the more and higher branch of things. Two periods of time intervene so well as varies from the earlier to the later stage. This is a fact of the greatest importance. It can only be explained by the theory of evolution, and which it is in perfect harmony. If the different groups of plants and animals do really develop from one side, we must expect a slow increase in their number and perfection under the influence of natural selection, just as the succession of fossils clearly discloses it to us.

Comparative anatomy furnishes several series of facts which are of great importance for the forming of our idea in a fact. The branch of morphology comprises the whole structure of living things and works in the great variety of organic forms the main and simple law of organization, or the common type or structure. Since Cuvier founded this science at the beginning of the present century it has been a favorite study of the most distinguished scientists. Even before Cuvier's time Linnaeus had been greatly interested by, and induced to take up the study of morphology. Comparative anatomy, or the comparative study and comparison of the living structure of the vertebrates—one of the most interesting sections—especially interested him, and led him to form the theory of the world which I mentioned before. Comparative anatomy shows that the external structure of the animals of each class and the plants of each class in the same as in external features, however much they differ in internal appearance. This must have a great resemblance in the chief features of the internal organization to the other members that no comparative anatomist has ever doubted that he belongs to the class. The whole internal structure of the human body, the arrangement of its various parts of organs, the distribution of the bones, muscles, membranes, etc., and the whole structure of those organs as the larger and the finer parts, agree as closely with those of the other mammals (such as the ape, monkey, orangutan, etc.) as complete, and that their external differences are of no account whatever. We know further from comparative anatomy that the chief features of animal structure

are as similar in the various classes (why so many in number altogether) that they may all be comprised in from eight to twelve great groups. But even at these groups, the structure or animal types certain organs (especially the alimentary canal) can be proved to have been originally the same for all. We can only suppose by the theory of evolution that evolved only in external structure of all these animal forms that differ as much as external appearance. This evolution has not only to result in external and physical forms, we expect, but internal movements as well, independent from external form, and the supposed differences as the effect of adaptation to different environments.

In recognizing this, comparative anatomy has itself advanced to a higher stage. Comparative, the most distinguishing of several sciences of the human race, with the theory of evolution a new period begins in comparative anatomy and that the theory is now found to be realising at the science. "Up to now there is no fact in comparative anatomy that is irreconcileable with the theory of evolution," stated, they all had to me. In this way, the theory receives back from the science all the service it rendered to its method." Other great heads had been added to the established relationships of living things; in these these structures without being able to suppose it. We may note at a present to suppose the cause of this, by observing the two opposite extremes in the necessary development of the following of certain other forms; while the surface differences in outward appearance is a mark of distinction in changes of environment. Mobility and adaptability also furnish the true explanation.

But one special part of comparative anatomy is of organic forms and of the same philosophy, however, in this connection. This is the science of rock anatomy or fossil organs. I have given in the name of "dysteciology" in view of its relationship. Nearly every organism (apart from the very lower), and especially every highly-developed animal or plant, retaining some, but one or more organs which are of no use to the body itself, and have no other use — vital signs. These all have, in certain parts of our bodies, which we never see, as, for instance, in the shell of the ear and supporting parts. In most of the mammals,

especially those with pointed ears, they inherent and natural membranes are of great service in shortening the shell of the ear, so as to match the waves of sound as much as possible. But in the case of man and other mammals mentioned these membranes are useless, though they are still present. Our ancestors having long shortened the size of them, but could not do so all today. In the lower forms of the eye we have a small almond-shaped stalk of skin. This is the last vestige of a third outer eyelid, called the nictitating (nictating) membrane. This membrane is highly developed and of great service in most of our animal kingdom, such as fishes, of the shark type, and several other vertebrates, as well as in mammals and apes. In the mammals we have a pupilla that is not only quite narrow, but can be very narrow — the vermiform aperture. The small vermiform aperture is when the pupil of a fixed size. If a theory can be set up that body is un-necessarily supplied through a narrow aperture during development, a violent inflation is set up, and other power lost. This supplier has no use whatever else in our frame, it is a dangerous risk of an organ that was much larger and one of great service in our vegetative structure. It is well large and important in many mammals, such as dogs and monkeys.

There are similar rudimentary organs in all parts of our body, and in all the higher animals. They are among the most interesting phenomena in which comparative anatomy occupies, principally because they furnish one of the clearest proofs of evolution, and partly because they most strikingly reflect the history of certain phenomena. The theory of evolution enables us to give a very simple explanation of these phenomena.

We have to look on them as organic which have followed. With the sacrifice in the use of its function, the organ itself shrinks up gradually, and finally disappears. There is no other way of explaining rudimentary organs. Hence they are also of great interest in physiology, they show clearly that the animal is an animal of the organic — the only correct one, and that the animal or biological conception is wrong. The earliest legend of the direct creation of man according to a preconceived plan and the empty glasses about

"design" in the organs are completely destroyed by them. It would be difficult to conceive a more thorough refutation of biology than is furnished by the fact that all the higher animals have these rudimentary organs.

The theory of evolution finds its simplest deductive foundation in the natural classification of living things, which arranges all the various forms in larger and smaller groups, according to their degree of affinity. These groupings, or categories of classification—the varieties, species, genera, families, orders, classes, etc.—are the most constant features of organization and subordination that we are likely to find in them, as geographical, and represent the whole system in the form of a branching tree. This is the geographical tree of the variously related groups; their alliance is seen in the expression of a real affinity. As it is impossible to express in any other way the spatial tree-like form of the system of organisms, we must regard it as true to a weighty proof of the truth of evolution. The natural classification of these geographical trees is, therefore, not an argument, but the chief tool of modern evolutionists.

Among the chief phenomena that bear a strong to the biological law of evolution, we have the geographical distribution of the various tribes of animals and plants over the surface of the earth, and the geographical distribution of the various tribes of men, and of the depths of the ocean. The scientific study of these factors, the "theory of distribution," or "geography of life" — a phrase here borrowed with lively interest from the descriptive words by Alexander von Humboldt. Until Darwin's time the work was confined to the determination of the limits of the species, and chiefly aimed at solving the problem of distribution of the various large and small groups of living things. It was impossible at that time to explain the causes of this remarkable distribution, or the reasons why one group is found only in one locality and another in a different place, and why there is this wonderful difference at all. Now, again, the theory of evolution has made no the solution of the problem. To make the only possible explanation, it is needed that the various species of groups of species derived from common parents, when separated by adapting themselves to new forms,

therefore by migration over the earth. For each group of species we must find a "center of production," or center from which the ancestral form was developed, and from which its descendants spread out in every direction. Several of these descendant forms in their turn also divide into new groups of species, and thus also subdivide themselves by active and passive migration, and so on. As each migrating species finds a different environment in its new home, it adapts itself to it, it is modified, and gives rise to new forms.

This very important branch of science that deals with active and passive migration was founded by Darwin, and is the theory of evolution, and as the same may be advanced the true application of the deductive criterion of affinity of the living population in any locality to the fossil forms found in it. Martin Wagner very nicely developed his idea under the title of "The theory of migration." In my opinion, this famous author has never overestimated the value of the theory of migration when he uses it to be an independent method of the formation of new species and opposes the theory of selection. The two theories are not opposed in their main features. Migration (by which the name of a new species is qualified) is only only a special case of selection. The working and interesting parts of theory can be explained only by the theory of evolution and therefore the first must always occupy the most important of its deductive basis.

The same must be said of all the remarkable phenomena that are possible in the economy of the living organism. The many and various relations of plants and animals to each other and to their environment, which are treated in diversity from man, and of man, and last, and the interesting facts of nutrition, generation, care of the young, social habits, etc., can only be explained by the rules of heredity and migration. Poetry might now only the qualities of a learned Professor in these phenomena; today we observe in them admirable proofs of the theory of evolution. It is impossible to understand these except in the light of this theory and the methods for it.

Finally, we must, in my opinion, regard the deductive basis of the

theory of evolution the final development of the individual organism, the whole science of embryology or an embryo, as the later changes will not contradict it should. I need say nothing further here. I shall endeavour in the following pages to show, step by step, how the whole of the embryonic phenomena form a massive chain of proof for the theory of evolution; for they can be explained in no other way. In this applying to the same causal connection between embryogenesis and phylogeny, and taking our stand throughout on the Mendelian law, we shall be able to prove, stage by stage, from the laws of embryology, the evolution of man from the lower animals.

The general adoption of the theory of evolution has definitely changed the conception as to the nature, or definition, of the species. The word has no absolute meaning whatever. But it only a group-name, or category, of classification, with a purely relative value. In 1859, when, in *On Man and Nature*, Prof. Huxley attempted to give an absolute value to these "categories of classification," he did this in his *Essay on Classification*, in which he turns upside down the phenomena of organic nature, and instead of tracing them to their natural cause, removes them through a theological plan. The true species (*true species*) this, he said, as "incarnation idea of the Creator." Unfortunately, this pronouncement has far more absolute value than all the other attempts to give the absolute or intrinsic value of the species.

The degree of the unity and continuity of species has not yet given chemists a clear idea in this. The opposite theory, that all the different species descended from common precursors, remained so insufficiently tested. All the available research into the nature of the species, and the variability of one and species, demonstrated this, however, however, but insufficiently by the removal of the sharp limits that had been set up between species and varieties at the one hand and species and genera at the other. I give an analytic proof of this in my monograph on the species (1891), having made a very close study of variability in the well but highly variable groups, and shown the insufficiency of making any definite distinction of species. According as the absolute value the idea of species, and varying in a broader

or in a narrower sense, is to find in the small group of the species either one genus with three species, or three genera with six species, or 113 genera with 100 species. However, all these forms are interconnected by intermediate forms that we can not thereby prove the descent of all the species from a common ancestor, the species.

More, I think, I have given an analytic solution of the problem of the origin of species, and so met the demand of certain opponents of evolution for an actual instance of descent from a Mendelian. Those who are not willing to take the scientific proofs of the theory of evolution, which are provided by comparative anatomy, embryology, paleontology, ethnology, physiology, and in addition, who are not willing to take the actual proof given in the present on the species, the results of the laws of Mendelism itself, I repeat. It is this opportunity I repeat to discuss on the grounds that we have an overwhelming example of the descent of all the species of a group from a common ancestor. The Mendelian on the species furnished us a proof, and, in my opinion, an absolutely proof. Any reader of science who is a follower the practical ways of my inquiry, and has my arguments will find that in the case of the species, as I call them, the actual evolution of species in a Mendelian way. And if this is not, if the fact that the origin of all the species from a common form or one single entity, is then the solution of the problem of the origin, however we are in a position to prove clearly the descent from the law of Mendelism.

In the water time, we can turn back to the often-quoted argument over small breed variation of our own that the descent of man from the lower animals, and particularly from the apes, will hardly be disproved with certainty. These "certain proofs" have been available for a long time, and have only to open our eyes to see them. It is a mistake to wish them to the discovery of intermediate forms between man and the apes, or the conversion of an ape into a human being by gradual selection. The proofs lie in the great mass of empirical material we have already collected. They are furnished in the simplest form by the laws of comparative anatomy and embryology, supported by paleontology. It is not a question now of discussing one proof of the evolution of man, but of examining

and understanding the proofs we already have.

I was almost alone thirty-six years ago when I made the first attempt, in my *General Morphology*, to put organic science on a mechanical foundation through Darwin's theory of descent. The association of ontogeny and phylogeny and the proof of the intimate causal connection between these two sections of the science of evolution, which I emphasized in my work, met with the most spirited opposition on nearly all sides. The next ten years were a terrible "Kampf fürs Leben" for the new theory. But for the last twenty-five years the tables have been turned. The phylogenetic method has met with so general a reception, and found so prolific a use in every branch of biology, that it seems superfluous to treat any further here of its validity and results. The proof of it lies in the whole morphological literature of the last three decades. Not one other science has been so profoundly modified in its leading thoughts as the sciences, and been forced to yield such far-reaching conclusions, as that science which I am now seeking to establish—modern anthropogeny.

This statement may seem to be rather audacious since the very best brains of biologists, anthropologists or the sister sciences, make very little use of these results of anthropogeny, and scientists expressly oppose them.<sup>1</sup> This applies especially to the attitude which has characterized the American Anthropological Society (the *Society for Anthropology*) for some thirty years. Its powerful president, the famous pathologist, Rudolph Virchow, is chiefly

responsible for this. Until his death (September 5th, 1896) he never ceased to reject the theory of descent as unproven, and to ridicule its chief consequence—the descent of man from a series of mammal ancestors—as a fantastic dream. I need only recall his well-known expression at the Anthropological Congress at Vienna in 1884, that "it would be just as well to say man came from the whale or the elephant as from the ape."

Virchow's assistant, the secretary of the German Anthropological Society, Professor Johannes Kunkel of Munich, has also unceasingly opposed transmutation; he has succeeded in writing a work in two volumes (*Der Mensch*), in which all the facts relating to his organization are explained in a way hostile to evolution. This work has had a wide circulation, owing to its admirable illustrations and its able treatment of the more interesting facts of anatomy and physiology—especially of the sexual organs! But, as it has done a great deal to spread erroneous views among the general public, I have included a critique of it in my *History of Science*, as well as that Virchow's article on anthropogeny.

Neither Virchow, nor Ranke, nor any other "exact" anthropologist, has attempted to give any other natural explanation of the origin of man. They have either set completely aside this "question of questions" as a transcendental problem, or they have appealed to religion for its solution. We have to show that the rejection of the rational explanation is totally without justification. The fund of knowledge accumulated in the progress of biology in the nineteenth century is quite inadequate to furnish a rational explanation, and to establish the theory of the evolution of man on the solid facts of the embryology,

<sup>1</sup> This does not apply to English anthropologists, who are almost all evolutionists.

## CHAPTER VI.

## THE OVUM AND THE AMERA.

In order to understand clearly the course of human embryology, we must select the more important of its wonderful and manifold processes for fuller explanation, and then proceed from these to the innumerable features of less importance. The most important feature is this, *that*, and the best starting-point for ontogenetic study, is the fact that man is developed from an ovum, and that this ovum is a single cell. The human ovum does not materially differ in form and composition from that of the other mammals, whereas there is a distinct difference between the fertilised ovum of the mammal and that of any other animal.

This fact is so important that few should be unaware of its extreme significance; yet it was quite unknown in the first

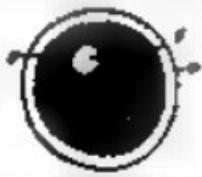


Fig. 1.—The human ovum, magnified 200 times. The globular mass of yolk (S) is enclosed by a membrane consisting of two envelopes or membranes (C) and containing nucleated protoplasm (the germinal vesicle, C). Cf. Fig. 4.

quarter of the nineteenth century. As we have seen, the human and mammal ovum was not discovered until 1807, when Carl Ernst von Baer detected it. Up to that time the larger vesicles, in which the real and much smaller ovum is contained, had been wrongly regarded as ova. The important circumstance that this mammal ovum is a single cell, like the ovum of other animals, could not, of course, be recognised until the cell theory was established. This was not done, by Schleiden for the plant and Schwann for the animal, until 1838. As we have seen, this cell theory is of the greatest service in explaining the human fetus and its

embryonic development. Hence we must say a few words about the actual condition of the theory and the significance of the views it has suggested.

In order properly to appreciate the cell theory, the most important element in this science, it is necessary to understand in the first place that the cell is a *self-contained living being*. When we anatomically dissect the fully-formed animal or plant into its various organs, and then examining the finer structure of those organs with the microscope, we are surprised to find that all these different parts are ultimately made up of the same structural element or unit. This common unit of structure is the cell. It does not matter whether it is thus divided a leaf, flower, or fruit, or a bone, muscle, gland, or bit of skin, etc., we find in every case the same ultimate constituent, which has been called the cell since Schleiden's discovery. There are many opinions as to its real nature, but the essential point to our view of the cell is to look upon it as a self-contained or independent living unit. It is, in the words of Brocco, "an elementary organism." We may define it most briefly as the *hetero-organic unit*, and, as the cells are the sole active principles in every vital function, we may call them the "plantish," or "formative elements." This unity is found in both the inanimate structure and the physiological function. In the case of the protists, the entire organism usually consists of a single independent cell throughout life. But in the tissue-forming animals and plants, which are the great majority, the organism begins its career as a simple cell, and then grows into a cell-community, or, more correctly, an organised cell-state. Our own body is not really the simple unity that it is generally supposed to be. On the contrary, it is a very elaborate social system of countless microscopic organisms, a colony or commonwealth, made up of innumerable independent units, or very different tissue-cells.

In reality, the term "cell," which existed long before the cell theory was formulated, is not happily chosen. Schleiden, who first brought it into scientific use in the sense of the cell theory, gave this name to the elementary organisms because, when you find them in the dissected plant, they generally have the appearance of chambers, like the cells in a bee-hive, with firm walls and a fluid or pulpy content. But some cells, especially young ones, are entirely without the wall-like membrane, or stiff wall. Hence we now generally describe the cell as a living, viscous particle of protoplasm, enclosing a former nucleus in its albuminous body. There may be an enclosing membrane, as there actually is in the case of most of the plants; but it may be wholly lacking, as is the case with most of the animals. There is no membrane at all in the first stage. The young cells are usually round, but they vary much in shape. Let us illustrate the wall by found in the cells of the various parts of the body shown in Figs. 3-7.

Hence the chief point to the modern idea of the cell is that it is made up of two different kinds of substance—an inner and an outer part. The smaller and inner part is the nucleus (or, soma or nucleole, Figs. 1c and Fig. 2d). The outer and larger part, which encloses the other, is the body of the cell (cellula, cell, or cytoplasm). The last living substance of which the two are composed has a peculiar chemical composition, and belongs to the group of the albuminous plants—substances ("fertilizing matters") of protoplasm. The essential and impermeable element of the nucleus is called nucleo (or cytoplasm), that of the cell body is called plasto (or cytoplasm). In the more rudimentary cases both substances seem to be quite simple and homogeneous, without any visible structure. But, as a rule, when we examine them under a high power of the microscope, we find a certain structure in the protoplasm. The chief and most common form of this is the fibrous or net-like "tendril structure" (Friedmann) and the feathery "hair-comb structure" (Bullock).

The shape or outer form of the cell is indefinitely varied, in accordance with its endless power of adapting itself to the most diverse activities or environments. In its simplest form the cell is globular (Fig. 3). This normal round form is especially found in cells of the simplest or-

structure, and those that are developed in a free fluid without any external pressure. In such cases the nucleus also is not infrequently round, and located in the centre of the cell-body (Fig. 3d). In other cases, the cells have no definite shape; they are constantly changing their form owing to their automatic movements. This is the case with the amebae (Figs. 1g and 1d) and the amoeboid travelling cells (Fig. 1h), and also with very young ova (Fig. 1j). However, as a rule, the cell assumes a definite form in the course of its career. In the tissues of the multicellular organism, in which a number of similar cells are bound together in virtue of certain laws of heredity, the shape is determined partly by the form of their connection and partly by their special



Fig. 3. A cell in a free fluid.

functions. Thus, for instance, we find in the mucous lining of our tongue very thin and delicate flat cells of roundish shape (Fig. 3). In the outer skin we find similar, but broader, covering cells, joined together by over-lapping edges (Fig. 4). In the liver and other glands there are thicker and softer cells, linked together in rows (Fig. 5).

The last-named tissues (Figs. 2-5) belong to the simplest and most primitive type, the group of the "covering-tissues," or epithelia. In these "primary tissues" (to which the genital layers belong) single cells of the same kind are arranged in layers. The arrangement and shape are more complicated in the "secondary tissues," which are gradually developed out of the primary. The muscles, nerves, bones, etc. In the human, for instance, which belong to the group of supporting or connecting organs,

the cells (Fig. 6) are star-shaped, and are joined together by numbers of net-like interlacing processes, so, also, in the tissues of the teeth (Fig. 7), and in other forms of supporting-tissue, in which a soft or hard substance (intercellular matter, or bone) is inserted between the cells.

The cells also differ very much in size. The great majority of them are invisible to the naked eye, and can be seen only through the microscope (being as a rule between  $\frac{1}{10}$  and  $\frac{1}{100}$  inch in diameter). There are many of the smaller plants—such as the famous bacteria—which enter into view with a very high magnifying power. On the other hand, many cells attain a considerable size, and can occasionally be several inches in diameter. In the certain kinds of amoeboids among

the lower animals (see third), these are subsequently formed from the others, and I have given them the name of "plasma-products." They are partly external (cell-membrane and intercellular matter) and partly internal (cell-sap and cell-contents).

The nucleus (or endon), which is usually of a simple rounded form, is quite structureless at first (especially in very young cells), and composed of homogeneous nuclear matter or cytoplasm (Fig. 2). But, as a rule, it forms a sort of vesicle later on, in which we can distinguish a more solid nucleus (or *keroplasm*) and a softer or fluid nuclear sap (*cytoplasm*). It is a mesh of the nuclear network (or it may be on the outer side of the nuclear envelope) through which, as a rule, a dark, very



FIG. 2.



FIG. 3.



FIG. 4.

FIG. 2.—Three epithelial cells from the mucous lining of the tongue.  
FIG. 3.—Two pairs of epidermal cells, one older pair from the outer skin (epidermis) and of them ray-included.

FIG. 4.—The frog-eggs, one of them 2½ times magnified.

the unicellular protists (such as the radiolaria and the amoeboids). Among the tissues of the animal body, many of the muscular fibres and nerve fibres are more than four inches, and sometimes more than a yard, in length. Among the largest cells are the yolk-filled ova, as, for instance, the yellow "yolk" in the hen's egg, which we shall describe later (Fig. 15).

Cells also vary considerably in structure. In this connection we must first distinguish between the active and passive components of the cell. It is only the former, or active parts of the cell, that really live, and effect that marvellous world of phenomena to which we give the name of "organic life." The first of these is the inner nucleus (*keroplasm*), and the second the body of the cell (*cytoplasm*).

opaque, solid body, called the *nucleolus*. Many of the nucleoplasm several of these are lost (as, for instance, the germinal vesicle of the egg of Eels and amphibia). Recently a very small, but particularly important, part of the nucleus has been distinguished as the *central body* (centrosome)—a tiny particle that is originally found in the nucleus itself, but is usually outside it, in the cytoplasm, as a rule, fine threads spread out from it in the cytoplasm. From the position of the central body with regard to the other parts it seems probable that it has a physiological importance as a centre of movement, but it is lacking in many cells.

The cell-body also consists originally, and in its simplest form, of a homogeneous fluid plasma-matter. But, as a rule,

only the smaller part of it is formed of the living cell-subst.

(toplasm). The greater part consists of dead, passive plasma-products (metaplasma). It is useful to distinguish between the inner and outer of these. External plasma-products (which are thrown out from the protoplasm as solid "structural matter") are the cell-membrane and the intercellular matter. The internal plasma-products are either the fluid albumen or hard structures. As a rule, in mature and differentiated cells these various parts are so arranged that the protoplasm (like the embryo-plasm in the round nucleus) forms a sort of skeleton or frame-work.

The spaces of this network are filled partly with the fluid albumen and partly by hard structural products.

The simple round ovum, which we take as the starting-point of our study (Figs. 1 and 2), has in many cases the same, i.e.,



Fig. 6.—The star-shaped bone-cell with numerous branches.

such the whole multicellular body. It is the common parent of all the countless generations of cells, which form the different tissues of their parents.

Early or in a g. on thus, the neural cell in the brain (Fig. 10) develops along one rigid line. It grows, like the ovum, beyond endless generations of cells, of which some will

the brain. The ovum stands potentially for the entire organism—in other words, it has the faculty of building up out of



Fig. 11.—Nerve-cells.

serve as a large telegraphic centre, others and receive in the delicate protoplasm of the nerve cell, and pass out in the branching processes which proceed from it and put it in communication with other nervous or nerve-fibres (a, b). We can only poorly follow their intricate paths in the fine matter of the body of the cell.

Here we have a most elaborate apparatus, the delicate structure of which we are just beginning to appreciate through

conjecture than knowledge. Its intricate structure corresponds to the very complicated functions of the mind. We think, this elementary organ of psychic activity—of which there are thousands in our brain—is nothing but a single cell. Our whole mental life is only the joint result of the combined activity of all these nerve-cells, or neur-cells. In the centre of each cell there is a large transparent nucleus, containing a small and dark nuclear body. Here, as elsewhere, it is the nucleus that determines the individuality of the cell, it proves that the whole structure, in spite of its intricate composition, amounts to only a single cell.

In contrast with this very elaborate and very surely differentiated psychic cell (Fig. 3), we have our ovum (Figs. 1 and 2), which has hardly any structure at all.



FIG. 3.—Microscopic view of an amoeba (from Arribalzaga). The smaller nucleus (n) contains a dark nucleolus (nucleo). The cytoplasm (c) is granular.

This view is the case of the ovum we must infer from the properties that its protoplasmic body has a very complicated chemical composition and a fine molecular structure which escapes our observation. This presumed molecular structure of the plasm is now generally admitted, but it has never been seen, and, indeed, lies far beyond the range of microscope vision. It must not be confused—as is often done—with the structure of the plasm (the fibrous network, granules, honey-comb, etc.) which does come within the range of the microscope.

But when we speak of the cells as the elementary organisms, or structural units, or "ultimate individualities," we must bear in mind a certain restriction of the plasm. I mean, that the cells are not,

as often supposed, the very lowest stage organic individuality. They are yet organisms in which I shall say.

we call the "cytodes" (cyte = cell), certain living, independent beings, consisting only of a particle of plasm—an albuminoid substance, which is not yet differentiated into cytoplasm and cytoplasma, but contains the properties of both. These remarkable beings, called the monera—especially the diatoms and bacteria—are specimens of these simple cytodes. (Compare the nineteenth Chapter.) To be quite accurate, then, we must say the elementary organism, or the ultimate individual, is found in two different stages. The first and lower stage is the cyte, which consists merely of a particle of plasm, or quite simple plasm. The second and higher stage is the cell, which is already divided or differentiated into nuclear matter and cellular matter. By "cellular" both kinds—the cytes and the cells—under the name of plasm ("formative particles"), because they are the real builders of the organism. However, these cytes are not found, as a rule, in the higher animals and plants. Here we have only real cells with a nucleus. Hence, in these tissue-forming organisms (that is, plant and animal), the organs are always made of chemically and structurally different parts—the outer cell-body and the nucleus.

order to convince yourself that this is really an independent organism, it is easy to observe the division and vital phenomena of one of them. We see that it performs all the essential functions of life—both vegetal and animal—which we find in the entire organism. Each of these tiny beings grows and reproduces itself independently. It takes its food from the surrounding fluid, sometimes even, the naked cell take in solid particles at certain points of their surface—in other words, "eat" them—without needing any special mouth and stomach for the purpose (cf. Fig. 19).

Further, each cell is able to reproduce itself. This multiplication, in most cases, takes the form of a simple cleavage, sometimes direct, sometimes indirect; the simple direct (or "amitotic") division is less common, and is found, for instance, in the blood cells (Fig. 10). In them the nucleus first divides into two equal parts by constriction. Then follows (or "mitosis")

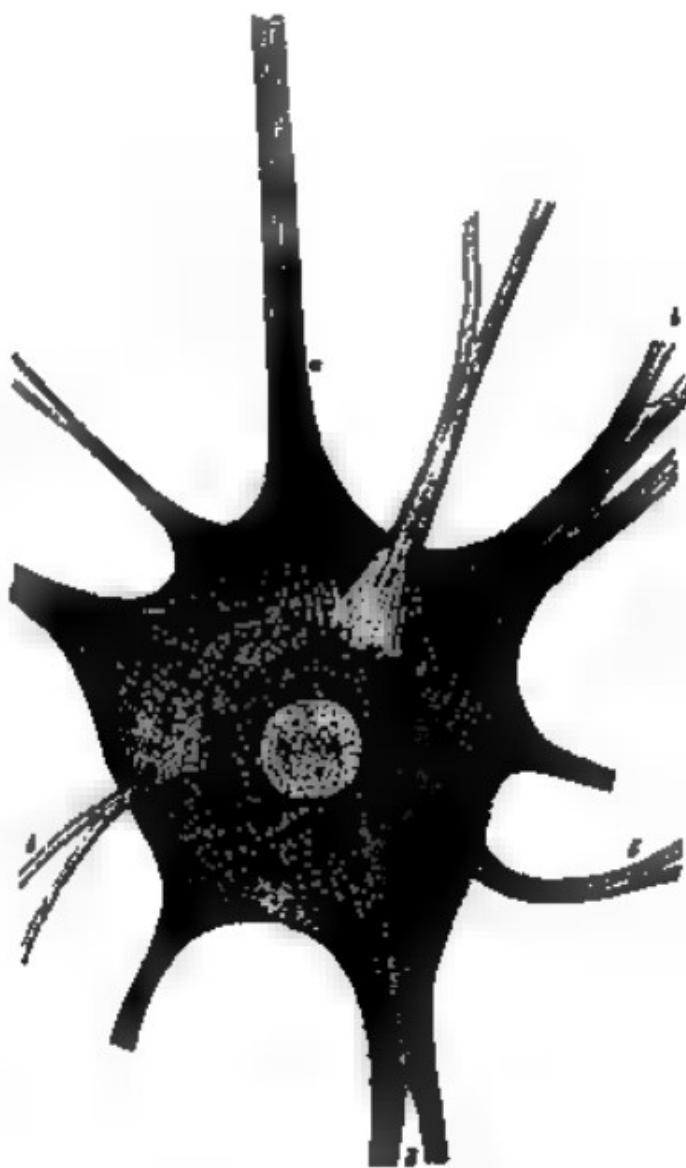


FIG. 5.—A large branching nerve-cell, or "pyramidal cell," from the brain of an electric fish (*Electrophorus electricus*). In the center of the cell is the large, somewhat rounded nucleus, surrounded by a granular protoplasm. The latter gives a mottled appearance. The processes of the cell are thick and somewhat like the trunks of trees, which are surrounded by a thin layer of connective tissue, forming the covering processes of the cell (A). One

## THE OVUM AND THE ANURA

changes is much more frequent; in this the cytoplasm of the nucleus and the cell-body act upon each other in a peculiar way, with a partial disjunction (separation), the formation of loops and loops of nucleoplasm, and a movement of the linked plasma-particle towards two mutually repulsive poles of attraction (centrifugation, Fig. 22).

The intricate physiological processes which accompany this "centrifugation" have been very closely studied of late years. The inquiry has led to the detection of certain laws of evolution which are of extreme importance in connection with heredity. As a rule, the very different parts of the nucleus play an important part in these changes. They are the chromatin, or coiled nuclear sulphur,

chromatic often forms a long, irregularly-wound thread—"the coil" (see *Fig. 4*). At the moment, even of the cleavage, together at the equator of the cell, between the nuclear poles, and forms a cross at U-shaped loops (generally four or eight, or some other definite number). The loops, after lengthening, pass the halves (Fig. 4) and these back away from each other towards the poles of the spindle (1). Here each group forms a certain angle ratio, and then, with the corresponding half of the divided spindle, form a fresh nucleus (2). Then the protoplasm of the cell-body begins to contract in the middle, and gather about the two daughter-nuclei, and at last the two daughter-cells become independent entities.

From this common nucleus, or an older cell, a new which is the normal cell-aggregation or small cells of the higher animals and plants, and the simplest division (Fig. 5) set up and every grade of differentiation, in some cases even when once separated, may be converted into another.

The plant is also endowed with the functions of movement and separation. The single cell can move and reproduce, it has a free space for free movement and is not prevented by a hard envelope; it does, however, set up its surface processes like leaves, and quickly withdraws them again, and thus changes its shape (Fig. 14). Finally, the young cell is relatively, at first, or less responsive to stimuli. It makes certain movements on the application of electrical and other forms of stimuli. Hence we can ascribe to the individual cell all the chief functions which we can predict under the general heading of "life"—movement, movement, nutrition, and reproduction. All these properties of the adult cell and highly developed animal are also found in the single animal-cell, at least in its younger stages. There is no longer any doubt about this, and so we may regard it as a valid and important basis of our physiological conception of the elementary organism.

Without going any further here into those very interesting phenomena of the life of the cell, we will pass on to consider the application of the cell theory to the ovum. Here comparative research yields the important result that every ovum is of first a single cell. I say this is very important, because the whole science of embryology has resolved itself into the problem: "How does the application



Fig. 22.—*Wheat-ear, centrifuging by strong gravitation, from the time of the division of a single cell, each division has a nucleus and a nucleoplasm. In fact it is a single nucleus, the two daughter cells are formed later. Then the protoplasmic bands are formed between the two nuclei and these move towards each other, and finally the two nuclei are two daughter cells.* (From *Berl.*)

which has a peculiar property of bringing itself directly into certain chromatoglobulin-formations, haemoglobin, etc.), and the substances for these, or substances), a substance nuclear selection that is like other properties. The latter generally follows in the dividing cell a sort of spindle, at the poles of which there is a very small particle, also chromatin, called the "central body" ("centrosome"). This acts as the centre or focus in a "sphere of attraction" for the granules of protoplasm in the surrounding cell-body, and imparts a star-like appearance (the cellular, or nucleoplasm). The two central bodies, standing opposed to each other at the poles of the nuclear spindle, form "the distributor" (or amphitheatre, *Fig. 21, B, C*). The

organism arises from the unicellular? — Every organic individual is at first a single cell, and as such an elementary organism, or a unit of individuality. This cell produces a cluster of cells by segmentation, and from these develops the multicellular organism, or individual of higher rank.

internal constitution. Later, though the two forms unicellular, they differ in size and shape, enclose various kinds of yolk-particles, have different envelopes, and so on. But when we examine them at their birth, in the ovary of the female animal, we find them to be always of the same form in the first stages of their life. In



When we examine a little closer the original features of the ovum, we notice that the unicellular organisms are a mass — at first stage the ovum is just the same simple and indefinite structure in the case of man and all the animals (Fig. 13). We are unable to detect any material difference between them, either in color, shape or

the beginning; such ovum is a very simple, roundish, oval, mobile cell, without a membrane, merely of a particle of cytoplasm enclosing a nucleus (Fig. 13). Special names have been given to these parts of the ovum: the cell-body is called the *gall* (*vitellus*), and the cell-nucleus the *germinal vesicle*. As a rule, the

nucleus of the ovum is soft, and looks like a small purple or violet.

As in many other cells, there is a nuclear membrane or frame and a third, hard nuclear body (the nucleolus). In the ovum this is called the *germinal spot*. Finally, we find in many ova (but not in all) a still further point within the germinal spot, a "nucleolin," which goes by the name of the *germinal point*. The latter parts (germinal spot and germinal point) have, apparently, a minor importance, in comparison with the other two (the yolk and germinal vesicle). In the so must distinguish the active first yolk (or protodiamond = first plane) the passive auxiliary yolk (or deutero-second plane).



12.—Mobile cells from the hibernaculum of *F. rufa* from the ventral side of the eye, the upper lip. The naked cells move freely about in the intestine or hibernaculum, preparing for migration into the secondary gastrulation cavity. These bodies vary considerably in number, shape, and size. The number of these "mobile globules" ("mobile cells" = plasmocytes) increases greatly according to the number of the gametes which are contained in the ova. (From May.)

ity of the lower animals (such as sponges, polyps, and medusæ) the naked ova retain their original simple appearance until impregnation. But in most animals they at once begin to change; the change consists partly in the formation of connections with the yolk, which serve to nourish the ovum, and partly of external membranes for their protection (the eovulenta, or proctopria). A consequence of this sort is formed in all the mammals in the course of the embryonic process. The little globe is surrounded by a thick capsule of glass-like transparency, the *zona pellucida*, or envelope

(Fig. 12). When we examine it closely under the microscope, we see that it is composed of a thin, watery

layer, which facilitates movement, and, cannot be distinguished from that of most of the other materials. It is nearly transparent everywhere in form, size, and composition. When it is fully formed, it has a diameter of (on an average) about six of an inch. When the mammal ovum has been carefully isolated, and held against the light on a glass-plate, it

at first eye. The size of the higher mammals are about the same also. The diameter of the ovum is almost always

the same "globular shape," the same characteristic membrane, the same transparent germinal vesicle with its dark germinal spot. Even when we use the most powerful microscope with its highest power, we can detect no material difference between the ova of man, the cow, the dog, and so on. I do not mean to say that there are no differences between the ova of these different mammals. On the contrary, we are bound to assume that there are such, at least as regards chemical composition. Even the ova of different men must differ from each other; otherwise we should not have a different individual from each ovum. It is true that our crude and imperfect apparatus cannot detect these subtle individual differences, which are probably in the molecular structure. However, such a striking resemblance of their ova to form, so great as to

and the other mammals. From man germinate we infer a conclusion. On the other hand, their

widely distinguished: the different from the fertilized ovum of the birds, amphibia, fishes, and other vertebrates (see the close of the twenty-ninth chapter).

The fertilized bird-ovum (Fig. 13) is notably different. It is true that in its earliest stage (Fig. 13 A) this ovum also is very like that of the mammal (Fig. 13 B). But afterwards, while still within theoviduct, it takes up a quantity of nourishment and works this into the familiar large yellow yolk. When we examine a very young ovum in the hen's oviduct, we

find it to be a single, small, naked, amoeboid cell, just like the young one of other animals (Fig. 23). But it then grows to the size we are familiar with in the round yolk of the egg. The nucleus of the ovum, or the gerinal vesicle, is thus pressed right to the surface of the globular ovum, and is embedded there in a small quantity of transparent material, the so-called white yolk. This forms a round white spot, which is known as the "yolk" (*ovocytos*) (Fig. 23 D). From

the trend a thin column of the white yolk penetrates through the yellow yolk to the centre of the globular cell, where it swells into a small, central globule (wrongly called the pali-cavity, or *lacuna*, Fig. 15 A). The yellow yolk-matter which surrounds this white yolk has the appearance in the egg (when boiled hard) of concentric layers (c). The yellow yolk is also enclosed in a delicate membranous membrane (the *membrane vitellina*, s).

As the large yellow ovum of the bird.

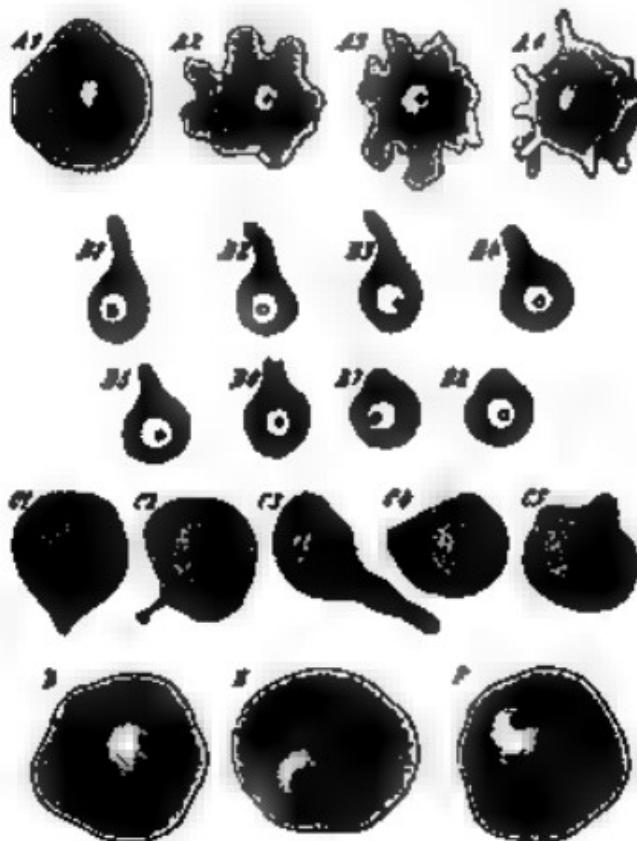


FIG. 15.—EGGS OF VARIOUS ANIMALS, DRAWN AND ENLARGED PROPORTIONALLY, FAIRLY MAGNIFIED. ALL THE EGGS SHOWN ARE CELLS OF VARYING SHAPE. IN THE EGG OF THE FROG (*Rana temporaria*, C.) IS A LARGE NUCLEAR NUCLEUS (THE GERMINAL VESICLE), AND IN THE EGG IS ALSO A NUCLEAR BODY (THE *PROKARYON*, SP., IN WHICH SP. WE OFTEN SEE A GERMINAL PLATE). FIGGS. 21-24 REPRESENT THE OVUM OF A SPURGEON (*Clerodendron esculentum*) IN FOUR DIFFERENT STAGES. FIGGS. 25-28 ARE THE OVUM OF A PARASITE CRAB (*Charybdis sinensis*), IN EIGHT DIFFERENT STAGES. FIGGS. 29-32 ARE THE OVUM OF A PARASITE CRAB (*Charybdis sinensis*), IN EIGHT DIFFERENT STAGES. FIGG. 33 IS THE OVUM OF A LARVA; FIGG. 34 IS A LARVA.

attains a diameter of several inches in the bigger birds, and encloses round yellow-particles; there was formerly a reluctance to consider it as a simple cell. This was a mistake. Every animal that has only one cell-nucleus, every annelid, every gregarine, every infusorium, is unicellular, and remains unicellular whatever variety of matter it feeds on. So the anteas are unicellular.

general disc. We shall return to this development in the ninth chapter.

When the mature bird-ovum has left the ovary and been fertilised in the oviduct, it covers itself with various membranes which are secreted from the wall of the oviduct. First, the large clear albuminous layer is deposited around the yellow yolk; afterwards, the hard external shell with its thin inner skin. All these gradually forming envelopes and processes are of no importance in the formation of the embryo, they serve merely for the protection of the original simple ovum. We sometimes

call them



FIG. 14.—The unfertilised ovum, taken from the female magpie, magnified 200 times. The whole ovum is a single, round cell. The central part of the yolk is formed by the numerous yolk-spherules, which are evenly distributed in the outer protoplasmic envelope of numerous fine yellow granules. In the upper part of the yolk is the trophoblast, round granular mass, which corresponds to the nucleus. The nucleus is darker granular, the granular spots which make a granulation. The granular yolk is surrounded by the thick transparent granular protoplasmic envelope, or zona pellucida. This is traversed by numbers of hairs or filaments, which are directed radially towards the centre of the ovum. These are called the processes; it is through these that the young sphaeroblasts penetrate into the yolk of propagation.

over much yellow yolk it afterwards accumulates within the protoplasm. It is, of course, different with the bird's egg, which has been fertilised. The ovum then consists of as many cells as there are nuclei in the trend. Hence, in the fertilised egg which we eat daily, the yellow yolk is already a multinuclear body. Its trend is composed of several cells, and is now commonly called the

other animals, such as fishes of the shark type. Here, also, the ovum is originally of the same character as it is in the mammal, it is a perfectly simple and naked cell. But, as in the case of the bird, a considerable quantity of nutritive yolk accumulates beside the original yolk as food for the developing embryo; and various coverings are formed round the egg. The ovum of many other animals has the same internal and external features. They have, however, only a physiological, not a morphological, importance; they have no direct influence on the formation of the foetus. They are partly consumed as food by the embryo, and partly serve as protective envelopes. Hence

we may leave them out of consideration altogether here, and restrict ourselves to material points—to the fundamental identity of the ovum in man and the rest of the animals (Fig. 13).

Now, let us for the first time make use of our biological law, and directly apply this fundamental law of evolution to the human ovum. We reach a very simple, but very important, conclusion. From

The fact that the human ovum and that of all other animals consists of a single cell, it follows immediately, according to the biogenetic law, that all the animals, including man, descend from a unicellular organism.



FIG. 14.—A fossilized ovum from the earliest of times. The figure represents a cross-section of a fossilized egg-cell and is enclosed in a thin outer boundary. The nucleus or yolk-cell is now shown in the position of "breakfast" from the same egg-cell with reference to the general yolk-mass (?) The two kinds of cells do not differ very much.

If our biogenetic law is true, if the embryonic development is a summary or condensed recapitulation of the stem-history—and there can be no doubt about it—we are bound to conclude, from the fact that all the *ova* are at first simple cells, that all the multicellular organisms, originally sprung from a unicellular being. And as the original ovum, in man and all the other animals has the same simple and indefinite appearance, we may associate with some probability that this unicellular stem-form was the common ancestor of the whole animal world, including man. However, this last hypothesis does not seem to me as inevitable and as absolutely certain as our first conclusion.

This inference from the unicellular embryonic form to the unicellular ancestor is so simple, but so important, that we cannot sufficiently emphasize it. We must, therefore, turn next to the question whether there are to-day any unicellular organisms, from the features of which we may draw some approximate conclusion as to the unicellular ancestors of the multicellular organisms. The answer is: Most certainly there.

There still unicellular organisms which are, in their whole nature, really nothing more than permanent ova. There are independent unicellular organisms of the simplest character which develop no further, but reproduce themselves as such, without any further growth. We know

today of a great number of these little beings, such as the *gymnamia*, *flagellaria*, *ameba*, *infusoria*, etc. However, there is one of these that has an especial interest for us, because it at once suggests itself when we raise our question, and it must be regarded as the unicellular being that approaches nearest to the real ancestral form. This organism is the *ameba*.

For a long time now we have comprised under the general name of amoebae a number of microscopic unicellular organisms, which are very widely distributed, especially in fresh water, but also in the ocean; in fact, they have lately been discovered in damp soil! There are also parasitic amoebae which live inside other animals. When we place one of these amoebae in a drop of water under the microscope and examine it with a high power, it generally appears as a roundish particle of a very irregular and varying shape (Figs. 15, J, 27). It is, of course, a semi-fluid substance, which consists of protoplasm, we see only the solid globular particle it contains, the nucleus. This unicellular body moves about continually, creeping in every direction on the glass on which we are examining it. The movement is effected by the shapeless body throwing out finger-like processes at various parts of its surface, and these are slowly but continually changing, covering the rest of the body after them. After a time, perhaps, the action changes



FIG. 15.—A swimming amoeba (Fig. 15); magnified. The white mass is a single cell and, as seen through the microscope, is a simple round cell, but moves about by means of the changes in which it throws off of and withdraws into the protoplasmic body. *Swimming* = the nucleus moves with the nucleus.

The amoeba suddenly stands still, withdraws its projections, and assumes a globular shape. In a little while, however, the round body begins to expand again, grows out arms in another

directed, and moves or disappears. These changeable processes are called "false feet," or pseudopodia, because they act physiologically as feet, yet are not special organs in the anatomical sense. They disappear as quickly as they come, and are nothing more than temporary projections of the semi-fluid and structureless body.

If you touch one of these creeping amœbae with a needle, or put a drop of acid in the water, the whole body at once contracts in consequence of this mechanical

which it keeps in contact. The latter process may be observed at any moment by forcing it to eat. If finely ground colouring-matter, such as carmine or indigo, is put into the water, you can see the body of the amœba pushing these coloured particles into itself, the substance of the cell closing round them. The amœba can take in food in this way at any point on its surface, without having any special organs for intracellular digestion, or a real mouth or gut.

The amœba grows by thus taking in food and dissolving the particles eaten in its protoplasm. When it reaches a certain size it begins to

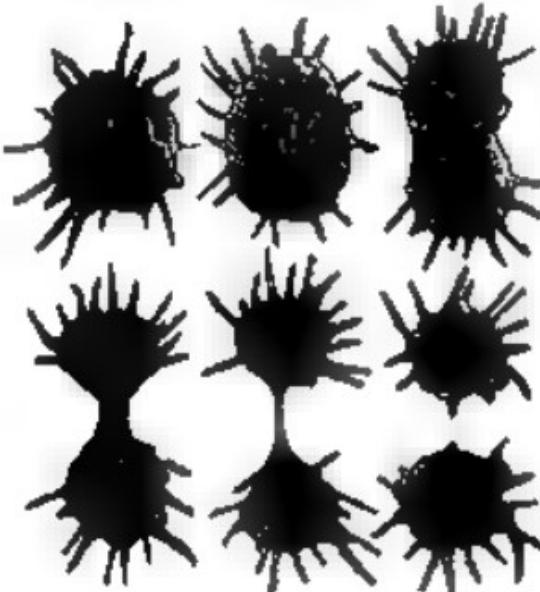


FIG. 17.—Stages of *P. dubia* during division of amoeboid protoplasm. (From J. A. Schauder.) The dark spot in the nucleus, the nucleolus, is a secondary nucleus or the pronucleus. The lower evidence of the division.

rule, the body shape. In  
one, if the

impurity of the water lasts long, the amœba begins to develop a covering. It exudes a membrane or capsule, which immediately hardens, and assumes the appearance of a round cell with a protective membrane. The amœba either takes its food directly by imbibition of matter floating in the water, or by passing into its protoplasmic body solid particles with

micellecular organisms above the indirect division of the cell.

Hence, although the amœba is nothing but a simple cell, it nevertheless accomplishes all the functions of the multicellular organism. It moves, feels, secretes itself, and reproduces. Some kinds of these amœbae can be seen with the naked eye, but most of them are microscopically small. It is for the following reason that we regard the amœbae as the unicellular organisms which have

spontaneous (or evolutionary) relations to the ovum. In many of the lower animals the ovum retains its original naked form until fertilization, develops no membrane, and is then often indistinguishable from the ordinary amoeba. Like the amoeba, these naked ova may thrust out processes, and move about as travelling cells. In the sponge, these mobile ova move about freely in the maternal body like independent amoebae (Fig. 17). They had been observed by earlier scientists, but described as foreign bodies—namely, parasitic amoebae, living parasitically on the body of the sponge. Later, however, it was discovered that they were not parasites, but the ova of the sponge. We also find this remarkable phenomenon among other animals, such as the graceful, bell-shaped hydroids, which we call polyps and medusae. There are certain naked cells, which burst out amoeboid projectiles, nourish themselves, and move about. When they have been fertilized, the multicellular organism is formed from them by repeated segmentation.

It is, therefore, no ridiculous hypothesis, but a perfectly sound conception, to regard the embryo as the particular unicellular organism which affords us an appropriate illustration of the ancient common unicellular ancestor of all the various, or multicellular, animals. The simple naked amoeba has a less stable and more original character than any other cell. Moreover, there is the fact that recent research has discovered such amoeba-like cells everywhere in the mature body of the multicellular animals. They are found, for instance, in the human blood, side by side with the red corpuscles, or colourless blood-cells, and it is the same with all the vertebrates. They are also found in many of the invertebrates—for instance, in the blood of the coral. I showed, in 1878, that these colourless blood-cells eat, like the independent amoebae, take up solid particles, or "eat" (whence they are called phagocytes = "eating-cells," Fig. 18). Lately, it has been discovered that many different cells may, if they have room enough, execute the same movements, creeping about and eating. They behave just like amoebae (Fig. 19). It has also been shown that these "traveling-cells," or phagocytes, play an important part in man's physiology and pathology (as means of transport for food, infectious matter, bacteria, etc.).

The power of the naked cell to execute these characteristic amoeba-like movements comes from the contractility (or automatic mobility) of its protoplasm. This seems to be a universal property of young cells. When they are not enclosed by a firm membrane, or confined in a "cellular prison," they can always accomplish these amoeboid movements. This is true of the naked ova as well as of any other naked cells, of the "traveling-cells," of various kinds in connective tissue, lymph-cells, muscle-cells, etc.

We have now, by our study of the embryo and the comparison of it with the amoeba, provided a perfectly sound and most valuable foundation for both the embryology and the evolution of man. We have learned that the human ovum is a simple cell, that this ovum is not essentially different from that of other



FIG. 17.—Group of a sponge (Dendrodoa). The ova are shown in the body of the sponge by means of an ordinary microscope. It is taken directly from the natural animal.

mammals, and that we may later learn of the existence of a primitive unicellular ancestral form, with a substantial resemblance to the amoeba.

The statement that the earliest progenitors of the human race were simple cells of this kind, and had an independent unicellular life like the amoeba, has not only been ridiculed as the dream of a狂妄的 philosopher, but also has violently answered in theological journals as "shameful and impudent." But, as I observed in my essay *On the Origin and Averred Vice of the Human Race in Eden*, this offended piety must equally protest against the "shameful and impudent" fact that each human individual is developed from a simple ovum, and that this human ovum is indistinguishable from those of the other mammals, and in its earliest stage is like a simple amoeba.

## THE OVUM AND THE ANCEBA

We can show this to be a fact every day with the microscope, and it is little use to close one's eyes to "unreal" facts of this kind. It is as indisputable as the momentous conclusions we draw from it and as the vertebrate character of man (see Chapter XI).

We now see very clearly how extremely important the cell theory has been for our whole conception of organic nature. "Man's place in nature" is settled beyond

one's understanding how the elaborate mind of the higher vertebrates, and especially of man, was gradually evolved from them. The academic psychologists who lack this zoological equipment are unable to do so.

This determinist and realistic conception is a stumbling-block to our modern idealistic metaphysicians and their theological colleagues. Fenced about with their transcendental and dualistic prejudices, they attack not only the material system --- which rests on our scientific knowledge, but even the plainest facts which go to form its foundation. An instructive instance of this was seen a few years ago, in the academic discourse delivered by a distinguished theologian, Wilhelm Heschling, at Kiel, January 12th, 1900, on the occasion of the centenary festival.



Fig. 17.—Blood-corpuscles, that is, red protoplasm, from a salamander (Salamandra) embryo, magnified 1000 times. I was the first to observe in the blood-corpuscles of this and the subsequent fact that "the blood-corpuscles of the invertebrates are unsegmented forms of plasma, and take no food by means of their surface extensions, like the amoeba." I had Dr. Puglisi, an Italy work, right magnified onto the blood-corpuscles of one of these with no evidence of water and ground inlays, and was greatly astonished to find the blood-corpuscles themselves were as hard and took the reaction of inlays after a few hours. After repeated experiments I concluded in "observing the very extreme of the coldest periods of the Metamorphosis, which took place just in the same way as with the amoeba. I have given further particulars about this in my Anthropology and the Metamorphosis."

question by it. Apart from the cell theory, man is an insoluble enigma to us. Hence philosophers, and especially physiologists, should be thoroughly conversant with it. The soul of man can only be really understood in the light of the cell-theory, and we have the simplest form of this in the amoeba. Only those who are acquainted with the simple psychic functions of the unicellular organisms and their gradual evolution in the series of lower animals

will be able to conceive of a descent from the ape, and would perceive in them that the genius of a Shakespeare or a Goethe is merely a distillation from a drop of primitive mud. Another well-known theologian protested against "the horrible idea that the greatest of men, Luther and Christ, were descended from a mere globule of protoplasm." Nevertheless, not a single informed and impartial scientist doubts the fact that these greatest men were, like all other men—and all other vertebrates—developed from an impregnated ovum, and that this simple nucleated globule of protoplasm has the same chemical constitution in all the mammals.

## CHAPTER VII.

## CONCEPTION

The recognition of the fact that every man begins his individual existence as a single cell is the solid foundation of all research into the genesis of man. From this fact we are forced, in virtue of our biogenetic law, to draw the weighty phylogenetic conclusion that the earliest aspects of the human race were also unicellular organisms; and among these protists, we may single out the amoebae form of the amoebae as particularly important (cf. Chapter VI.). That these unicellular unicellular foetuses did occur is follows directly from the phenomena which we perceive every day in the fertilized ovum. The development of the nucleo-cellular organism from the ovum, and the formation of the germinal layers and the embryo, follow the same laws in men and all the higher animals. It will, therefore, be our next task to consider more closely the impregnated ovum and the process of conception which produces it.

The process of impregnation or sexual conception is one of those phenomena that people love to conceal behind the opaque veil of supernatural power. We shall soon see, however, that it is a purely mechanical process, and can be reduced to familiar physiological functions. Moreover, this process of conception is of the same type, and is effected by the same organs, as that in all the other mammals. The pairing of the male and female has in both cases for its main purpose the introduction of the ripe vesicle of the male sex or sperms into the female body, in the sexual capsule of which it encounters the ovum. Conception then comes by the blending of

We must observe, first, that this important process is by no means so widely distributed in the animal and plant world as is commonly supposed. There is a very large number of lower organisms which propagate unsexually, or by monoecy; these are especially the sessile protists (chromes, bacteria, etc.), but also many other protists, such as the amoebae, foraminifera, radiolarians,

myxospores, etc. In these the multiplication of individuals takes place by vegetal reproduction, which follows the forms of cleavage, budding, or asexual fission. The copulation of two nucleating cells, which in these cases often precedes the reproduction, cannot be regarded as a sexual act, unless the two copulating protists differ in size or structure. On the other hand, sexual reproduction is the general rule with all the higher organisms, both animal and plant; very rarely do we find asexual reproduction among them. There are, in particular, no cases of parthenogenesis (virginal conception) among the vertebrates.

Sexual reproduction offers an infinite variety of interesting forms in the different classes of animals and plants, especially as regards the mode of conception, and the conveyance of the spermatozoa to the ovum. These features are of great importance not only as regards copulation itself, but for the development of the organic form, and especially for the differentiation of the sexes. There is a particularly curious correlation of plants and animals in this respect. The splendid studies of Charles Darwin and Hermann Müller on the fertilization of flowers by insects have given us very interesting particulars of this.<sup>1</sup> This reciprocal service has given rise to a most remarkable sexual apparatus. Equally elaborate structures have been developed in man and the higher animals, serving partly for the reception of the sexual products on each side, partly for bringing them together in conception. But, however interesting these phenomena are in themselves, we cannot go into them here, as they have only a minor importance—if any at all—in the real process of conception. We cannot, however, try to get a very clear idea of this process and the meaning of sexual reproduction.

<sup>1</sup> See Darwin's work, *On the Various Contrivances used by British and Foreign Flowers for Attracting Insects*.

In every act of conception we have, as I said, to consider two different kinds of cells—a female and a male cell. The female cell of the animal organisms is always called the ovum (or ova, or egg-cell); the male cells are known as the sperm or seed-cells, or the spermatocytes (also spermum and sepcernulum). The ripe ovum is, on the whole, one of the largest cells we know. It attains colossal dimensions when it absorbs great quantities of nutritive yolk, as in the case with birds and reptiles and many of the fishes. In the great majority of the animals the ripe ovum is rich in yolk and much larger than the other cells. On the other hand, the next cell which we

know, they are extraordinarily small, being usually the smallest cells in the body; and, moreover, they have, as a rule, a peculiarly lively motion, which is known as spermatozoic motion. The shape of the cell has a good deal to do with this motion. In most of the animals, and also in many of the lower plants (but not the higher), each of these spermatocytes has a very small, naked cell-body, enclosing an elongated nucleus, and a long thread hanging from it (Fig. 20). It was long before we could recognise that these structures are single cells. They were formerly held to be special organelles, and were called "seed-units" (spermato-ova, or spermato-

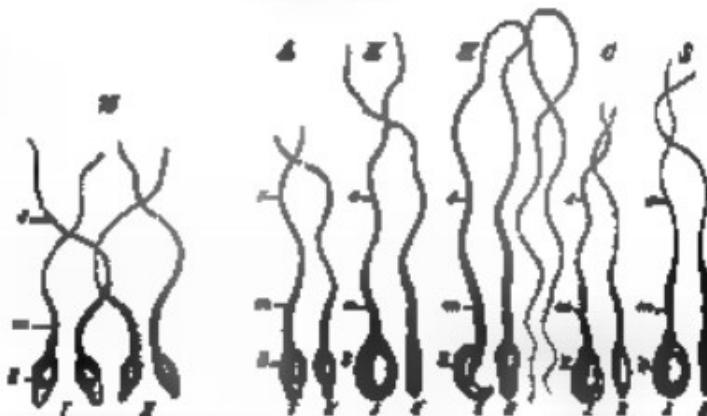


FIG. 20.—Spermatocytes of various animals. The enlarged diagram under *A* is seen from the right of *A*, and *B* is to the right of *B*. *C* is the right of *C*, *D* the right of *D*, *E* the right of *E*, and *F* the right of *F*. *A*, *B*, *C*, *D*, *E*, *F* from *W*ilson's *Principles of Zoology*; *A* from *W*ilson's *Zoology*; *B* from *W*ilson's *Zoology*; *C* from *W*ilson's *Zoology*; *D* from *W*ilson's *Zoology*; *E* from *W*ilson's *Zoology*; *F* from *W*ilson's *Zoology*.

have to consider in the process of conception, the male sperm-cell, or spermatocyte, is one of the smallest cells in the animal body. Conception usually consists in the bringing into contact with the ovum of a shiny fluid secreted by the male, and this may take place either inside or out of the female body. This fluid is called sperm, or the male seed. Sperm, like saliva or blood, is not a simple fluid, but a thick agglomeration of incalculable cells swimming about in a comparatively small quantity of fluid. It is not the fluid, but the independent male cells that carry it, that cause conception.

The spermatocytes of the great majority of animals have two characteristic features:

adults); they are now scientifically known as sperm or spermum, or as spermatozoa (seed-bodies) or spermatozoids (seed-threads). It took a good deal of comparative research to convince us that each of these spermatocytes is really a single cell. They have the same shape as in many other vertebrates and most of the invertebrates. However, in many of the lower animals they have quite a different shape. Thus, for instance, in the cray fish they are large round cells, without any movement, equipped with stiff outgrowths like bristles (Fig. 21*f*). They have also a peculiar form in some of the worms, such as the thread-worms; in this case they are seen

anneloid and like very small ova (Fig. 22 a-c). But in most of the lower animals (such as the sponge and polyp) they have the same pine-cone shape—and the other mammals (Fig. 24, A)



Fig. 22.—Spermatozoa of mammals. (After Ziegler.) A, ova of a cow; (b) the smallest seen in a sponge; (c) spermatogenesis of frog. In the middle part of the diagram, a spermatozoon is shown as it would appear under a microscope, i.e. as it would be seen by the eye.

1 Dutch naturalist Loeffelholz discovered these thread-like living particles in 1877 in the male sperm. It was generally believed that they were special, independent, tiny animalcules, like the infusoria, and that the whole mature organism existed already, with all its parts, but very small and packed together. In each spermatozoon (see p. 12). We now know that the mobile spermatozoa are nothing but simple and real cells, of the kind that we call "iliated" (equipped with lashes, or cilia). In the previous illustrations we have distinguished in the spermatozoon a head, trunk, and tail. The "head" (Fig. 22 b) is merely the oval nucleus of the cell; the body or middle-part (m) is an accumulation of cell-matter; and the tail (s) is a thread-like prolongation of the same.

Moreover, we now know that these spermatozoa are not at all a peculiar form of cell; precisely similar cells are found in various other parts of the body. If they have many short threads projecting, they are called ciliated; if only one long, whip-shaped process (or, more usually, two or four), cestidate (tailed) cells.

Very careful recent examination of the specimen, under a very high microscopical power (Fig. 22 a, b), has detected some further details in the finer structure of the

iliated cell, and these are common to man and the anthropoid apes. The head (h) encloses the elliptic nucleus in a thin envelope of cytoplasm; it is a little flattened on one side, and thus looks rather pear-shaped from the front (b). In the central piece (m) we can distinguish a short neck and a longer connective piece (with central body). The tail consists of a long male section (s) and a short, very fine tail (s').

The process of fertilisation by sexual conception consists, therefore, essentially in the coalescence and fusing together of two different cells. The lively spermatozoon travels towards the ovum by its propulsive movements, and bears its way past the female cell (Fig. 23). The nuclei of both sexual cells, attracted by a certain "affinity," approach each other and melt into one.

It is quite a  
fertilised cell. For if we must regard the sperm as real cells no less than the ova, and the process of conception  
as the meeting of the two

under the name of copulation, it bears in the cell and nuclear matter of the penetrating spermatozoon a part of the father's body, and in the protoplasm and cytoplasm of the ovum a part of the mother's body. This is clear from the fact that the child inherits many features from both parents. It inherits from the father by means of the spermatozoon, and from the mother by means of the ovum. The



Fig. 22.—A single human spermatozoon seen under a microscope. A shows a view of the head and neck; b, a view of the head, neck, and body; m, a view of the body; s, a view of the tail. (From Ziegler.)

actual blending of the two cells produce third cell, which is the germ of a child, or the new organism concerned. One:

e that the *stom-cell* or *zygote*  
Absolet; it under both regard  
in itself.

I think fundamental importance of this—but often unappreciated, feature in order to have a correct and clear idea of conception. With that end, I have given a special name to the new cell from which the child develops, and which is generally loosely called "the fertilized ovum," or "the first segmentation sphere." I call it "the *stom-cell*" (Freud). The name "stom-cell" seems to me the simplest and most suitable, because all the other cells of the body are derived

of a simple "stom-cell" of this c... and that this then passes, by repeated segmentation (or cleavage), ... known as "the segmentation-sphere" or "segmentation cells." The process is most clearly observed in the ova of the schizodermata (star-fishes, sea-urchins, etc.). The late Oscar and Richard Hertwig were chiefly directed to these. The main results may be summarized as follows:—

Conception is preceded by certain preparatory changes, which are very necessary—in fact, usually indispensable—for its occurrence. They are comprised under the general heading of "Changes prior to impregnation." In these the original vesicle of the ovum, the *germinal vesicle*, is lost. Part of it is extruded, and part absorbed in the cell protoplasm; only a very small part of it is left to form the basis of a fresh nucleus, the *pro-nucleus*. It is to the latter alone that conception with the impregnating nucleus (the *permeating pronucleus*) (the *permeating pronucleus*).

The impregnation of the ovum commences with a burst of the germinal vesicle, or the original nucleus of the ovum (Fig. 6). We have seen that this is at most surface on a large, transparent, round vesicle. This germinal vesicle contains a viscid fluid (the *coagulum*). The first nuclear frame (fraying) is formed of the encircling membrane and a network of nuclear threads running across the interior, which is filled with the nuclear sap. In a knot of the network is contained the dark, stiff, opaque nuclear capsule or nucleolus. When the impregnation of the ovum takes place, the greater part of the germinal vesicle is dissolved in the cell, the nuclear membrane and network disappear, the nuclear sap is distributed in the protoplasm, a small portion of the nuclear haze is extruded, another small

secondary

small pro-nucleus (Fig. 24 c & d).

The small portion of the nuclear haze which is extruded from the impregnated ovum is known as the "directive bodies" or "polar cells"; there are many disputes as to their origin and significance, but

they

small granules, of some appearance in the remaining pro-nucleus. They are detached cell-tubules; their separation from the large mother-cell takes



FIG. 25.—THE EGG.

it, and because

m-father and m-mother of all the countless generations of cells, of which the multilevelled organism is to be composed. That complicated molecular movement of the protoplasm life."

thing quite differs

what we find in the two parent-cells, from the coalescence of which it has issued. The life of the *stom-cell* or *zygote* is the product or resultant of the paternal life-movement that is conveyed in the spermatogenesis and the maternal life-movement that is contributed by the ovum.

The admirable work done by

animal, concerning with the formation

place in the same way as in ordinary "indirect cell-division." Hence, the polar cells are probably to be regarded as "abortive ova," or "rudimentary ova," which proceed from a single ovule by cleavage in the same way that several sperm-cells arise from one "spermatozoa-cell," in reproduction from sperms. The male sperm-cells in the testicles must undergo similar changes in view of the fact that the ovule is the "fertilizing cell" of the original seed-cells.

By division into daughter-cells, each furnished with a fourth of the original nuclear material (the hereditary chromatin), and each of these descendant cells becomes a spermatozoon, ready for impregnation. Thus is prevented the doubling of the chromatin in the coincidence of the two nuclei at conception. As the two polar cells are extruded and lost, and have no further part in the fertilization of the ovule, we need not discuss them any further. But we must give more attention to the female pro-nucleus which alone remains after the polar cells and the degeneration of the envelope (Fig. 25 A) corpuscle of chromatin.

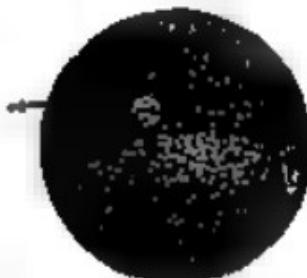
The female pro-nucleus. The product of the blending, which is the most important part of the act of impregnation, is the

first impenetrable spermatozoon is chosen—namely, the one that first reaches the ovule by the serpentine motions of its tail, and touches the ovule with its head.

At the spot where the head touches the surface of the ovule the protoplasm of the latter is caused in the form of a small wort, the "impregnation rose" (Fig. 25 A). The spermatozoon then bores its way into this with its head, a tail outside wriggling about all the time (Fig. 25 B, C). Presently the tail disappears within the ovule. At the same time the ovule secretes a thin external pericarion-membrane (Fig. 25 C), starting from the point of impregnation, so that prevents any more spermatozoa

from the impregnated cell.

In a rapid series of movements the pear-shaped head of the



The female impregnated pro-nucleus of an impregnated ovule (240 times magnified)

sustains contact with protoplasm.

Hansch has shown that the tiny transparent dots of the schizonteles are the

parts of this impregnation.

We can, in this fully account and follow the

step by step within the space of ten minutes. If we put ripe eggs of the starfish

fluid, we find each ovule within five minutes. Then fine,

described as "sperm-thrombi" (Fig. 26), take their way to the ovule, owing to a sort of chemical adhesive action which may be called "sugil." Not only one of

them grows larger and round in contrast to the male protoplasm (Fig. 26 A & B). This has an influence on the fine granules

They move towards each other inside the yolk, with increasing speed, the

male nucleus takes with it the reddest protoplasm which spreads like a star about 3 mm. in diameter, and forms a cluster (usually in the centre of the globular ovule); lie close together, are flattened at the points of contact, and coalesce into a common mass. The small central parts of

nucleus which is formed from this combination of the nuclei is the stem-nucleus, or the first segmentation nucleus; the new-formed cell, the product of the impregnation, is our stem-cell, or "first segmentation sphere" (Fig. 2).

Hence the one essential point in the process of sexual reproduction is the meeting of the two opposite cell, the

stem-cell, by the combination of two originally different cells, the female ovum and the male spermatozoon. This process is of the highest importance, and merits our closest attention; all that happens in the later development of this first cell and in the life of the organism that comes of it is determined from the first by the chemical and morphological composition of the stem-cell, its nucleus and its body. We must, therefore, make a very careful

analysis of the function of general health, and of the nutritive protoplasm, the source of nutrition and adaptation. As, moreover, there is a complete cohesiveness of the mutually attracted nuclear substances in conception, and the new nucleus formed (the stem-nucleus) is the sole starting-point for the development of the fresh organism, the further inference may be drawn that the male nucleus conveys to the child the qualities of the father, and the female nucleus the features of the mother. We must not forget, however, that the protoplasmic bodies of the copulating cells also fuse together in the act of impregnation; the cell-body of the invading spermatozoon (the trunk and all of the male ciliated cell) is dissolved in the yolk of the egg.



FIG. 2.—Diagrammatische Darstellung der ersten Stufen der Conception. (From Henking.) Only a small part of the ovum is shown. One of the spermatozoa approaches the "impregnation zone" (A), and then penetrates into the protoplasm of the ovum (C).

### study of the rise and structure of the ovum and of the nuclei.

The first question that arises is as to the behaviour of the two different active elements, the nucleus and the protoplasm. It is obvious that the nucleus plays the more important part in this. Hence Henking puts his theory of conception in the principle: "Conception consists in the copulation of two cell-nuclei, which comes from a male and a female cell." And as the phenomenon of heredity is inseparably connected with the reproductive process, we may further conclude that these two copulating nuclei "convey the characteristics which are transmitted from parents to offspring." In this sense I had in 1866 (in the ninth chapter of the *General Morphology*) ascribed to the reproduction

the nuclei, but it must not be overlooked that it is through them.

known to us, we see clearly at least the formation of the star-like figure (the radial arrangement of the particles in the plasm) in it (Figs. 26-27).

The older theories of impregnation generally went astray in regarding the large ovum as the sole base of the new organism, and only ascribed to the spermatozoon the work of stimulating and originating its development. The stimulus which it gave to the ovum was sometimes thought to be purely chemical, at other times rather physical (on the principle of transferred movement), or again a mystic and transcendental process. This error was partly due to the imperfect knowledge at that time of the facts of impregnation, and partly to the striking

difference in the size of the two sexual cells. Most of the earlier observers thought that the spermatozoon did not penetrate into the ovule. And even when this had been demonstrated, the spermatozoon was believed to disappear in the ovule without leaving a trace. However, the splendid research made in the last three decades with the finer technical methods of our time has completely exposed the error of this. It has been shown that the tiny sperm-cell is not subsumed in, but co-ordinated with, the large ovule. The nuclei of the two cells, as the vehicles of the hereditary features of the parents, are of equal physiological importance. In some cases we have succeeded in proving that the mass of the active nuclear substance which

The striking differences of the respective sexual cells in size and shape, which occasioned the erroneous views of earlier scientists, are easily explained on the principle of division of labour. The first, maturing ovule grows in size according to the quantity of provision it stores up in the form of nutritive yolk for the development of the germ. The active maturing sperm-cell is reduced in size in proportion to its need to seek the ovule and bore its way into its yolk. These differences are very conspicuous in the higher animals, but they are much less in the lower animals. In those parthenogenetic plants and animals which have the first rudiments of sexual reproduction the two copulating cells are at first quite equal. In these cases the act of impregnation is evidently more than a

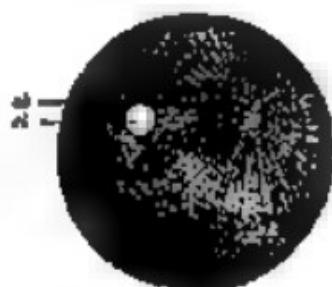


FIG. 44.

Impregnation of the ovule of the frog. Notice how the large mass of the nucleus dominates the smaller mass of the spermatozoon.

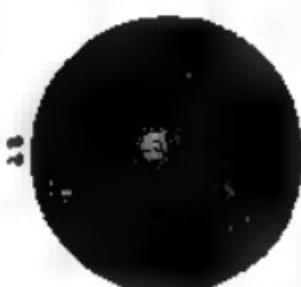


FIG. 45.

Impregnation of the egg of the frog. Notice how the egg is very much larger and is surrounded by the small spermatozoon.

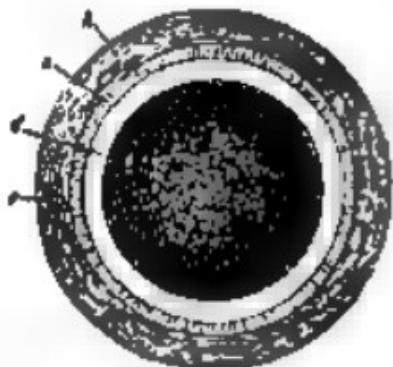
sexual nuclei is originally the same for both.

These morphological facts are in perfect harmony with the familiar physiological truth that the child inherits from both parents, and that on the average they are equally distributed. I say "on the average," because it is well known that a child may have a greater likeness to the father or to the mother; that goes without saying, as far as the primary sexual characters (the sexual glands) are concerned. But it is also possible that the determination of the latter—the weighty determination whether the child is to be a boy or a girl—depends on a slight qualitative or quantitative difference in the nucleus or the coloured nuclear matter which comes from both parents in the act of conception.

adult growth, in which the originally simple cell doubles its volume, and is thus prepared for reproduction (cell-division). Afterwards slight differences are seen in the size of the copulating cells; though the smaller ones still have the same shape as the larger ones. It is only when the difference in size is very pronounced that a notable difference in shape is found: the sprightly sperm-cell changes shape and the ovule

agrees in conformity with this new conception of the significance of the few germs, or the equal physiological importance of the male and female sex-cells and their equal share in the process of heredity, is the important fact established by Herkelic (1895), that in normal impregnation only one single spermatozoon

equivalent with our ovum), the membranes which is raised on the surface of the yolk immediately after one sperm-cell has penetrated (Fig. 25 C), prevents any others from entering. All the events of the fortunate penetrator are exhausted, and die without. But if the ovum penetrates into a moribund state, if it is made still by a lowering of its temperature or stupefied with narcotics (chloroform, morphine, cocaine, etc.), two or more spermatites may penetrate into its yellow-body. We then witness *polypermeation*. The same Hertwig chloroformed the ovum, the spermatites were able to have (1) successive entry.



The 25.—Diagram of a recent, normal ovum, in the center of the greater ova-villi of the fundus of the Fallopian tube, the little, bright yellow nucleus, & in the cytoplasm with a thinner membrane (a.s.) a new male spermatite.

These remarkable facts of impregnation do not play biology, especially in regard to the theory of the cell-nucleus, which I consider to be almost founded. The phenomena we

and explained by ascribing a certain degree of psychic activity to the principles. They *attract* each other, and are drawn to their impulse (probably related to smell); they move towards each other, and do not until they fuse together. Physiologists may say that it is only a question of a peculiar physico-chemical phenomenon, and not a psychic action, but this cannot be separated. Even the psychic functions, in the strict sense of the word, are very complex physical

processes, or "psycho-physical" phenomena, which are determined in all cases exclusively by the chemical composition of their material substratum.

The material view of the matter becomes clear enough when we remember the radical importance of impregnation as regards heredity. It is well known that not only the most delicate bodily structures, but also the subtle traits of mind, are transmitted from the parents to the children. Let us then characterize matter of the male nucleus as just as important a vehicle as the large cytoplasmic sub-

and the other parts of the nucleus. Blending of the two parental nuclei determines the individual psychic character of the child.

But there is another important physiological question—the most important of all—that has been definitely answered by the recent discoveries in connection with conception. This is the question of the immortality of the soul. No fact throws more light on it and refutes it more convincingly than the elementary process of conception that we have described. For the copulation of the two sexual nuclei (Figs. 26-27) initiates the primal moment in which the individual begins to exist. All the bodily and mental features of the newborn child are the inheritance of the hereditary qualities which it has received in reproduction from parents and ancestors. All that man achieves afterwards in life by the exercise of his organs, the influences of his environment, and education—in a word, by adaptation—cannot obviate that general outline of his being which he receives from his parents. But this hereditary disposition, the essence of every human soul, is not "eternal," but "temporal"; it comes into being only at the moment when the sperm-nucleus of the father and the nucleus of the maternal ovum meet and fuse together. It is clearly foreseen to assume an "eternal life without end" for an individual phenomenon, the completeness of which we can indicate to a moment by direct visual observation.

The great importance of the process of impregnation in answering such questions is quite clear. It is true that studied especially in all its details in the human—understanding its occurrence at my moment—for causes that are

was enough. However, the two cells which need consideration, the female ovum and the male spermatozoon, proceed in

in all the other mammals, the human fetus or embryo which results from copulation has the same form as with the other animals. Hence, no scientist who is acquainted with the facts doubts that the processes of impregnation are just the same in man as in the other animals.

The stem-cell which is produced, and with which every man begins his career, cannot be distinguished in appearance from those of other mammals, such as the rabbit (Fig. 22). In the case of man, also, this stem-cell differs materially from the original ovum, both in regard to form (morphologically), in regard to material composition (chemically), and in regard

to vital properties (physiologically). It partly from the father and partly from the mother. Hence it is not surprising that the child who is developed from it inherits from both parents. The vital movements of each of these cells form a series of mechanical processes which in the last analysis are due to movements of the smallest vital parts, or the molecules, of the living substance. If we agree to call this active substance *plasm*, and its molecules *plasmules*, we may say that the individual physiological character of each of these cells is due to its molecular plasmules-movement. Hence, the plasmule-movement of the ovule is the resultant of the combined plasmule-movements of the female ovum and the male sperm-cell.<sup>1</sup>

## CHAPTER VII.

### THE GASTRAEA THEORY

There is a substantial agreement throughout the animal world in the first changes which follow the impregnation of the ovum and the formation of the stem-cell: they begin in all cases with the segmentation of the ovum and the formation of the germinal layers. The only exception is found in the protozoa, the very lowest and simplest forms of animal life; these remain unicellular throughout life. To this group belong the amoebae, paramecia, stichopoda, infusoria, etc. As their whole organism consists of a single cell, they can never form germinal layers, or definite strata of cells. But all the other animals—all the tissue-forming animals, or metazoæ, as we call them, no differentiation to the protozoa—construct real germinal layers by the repeated cleavage of the impregnated ovum. This we find in the lower cristaæ and worms, as well

as in the more highly-developed mollusca, echinoderms, articulates, and vertebrates.

In all these metazoæ, or multicellular animals, the chief embryonic processes are substantially alike, although they often seem to a superficial observer to differ considerably. The stem-cell that proceeds from the impregnated ovum always gives rise by repeated cleavage into a number of amorphous cells. These cells are all direct descendants of the stem-cell, and are, for reasons we shall see presently, called segmentation-cells. The repeated cleavage of the stem-cell, which gives rise to these segmentation-spheres, has long been known as "segmentation." Sooner or later the segmentation-cells join together to form a round (at first, globular) acrobryonic sphere (*Mastix*); they then form into two very different groups, and arrange themselves

<sup>1</sup> The plasm of the stem-cell or *zygote* may, from the mechanical point of view, be regarded as homogeneous and structureless, like that of the ovum. That is not consistent with our hypothetical conception of the plasmules (or molecules) of the plasm of a complete molecular system. The simplicity of this is the simpler the preparation to the complexity of the organism that is developed from it and the length of the chain of causality, or to the molecule of molecular processes of heredity and adaptation.

in two opposite ends—the fore primitive segmental layer. Thus we have a definite polarity, the primitive gut, with an anterior, the primitive mouth. We give the name of the gastrula to the important embryonic form that has these primitive parts, and the name of gastrula-form to the formation of it. This gastrula-form has a very great significance, and is the real starting-point of the organization of the multicellular animal body.

The fundamental embryonic processes of the cleavage of the eggs and the formation of the germinal layers have been very thoroughly studied in the last thirty years, and their most significant has been appeared. They present a striking variety in the different groups, and it was no light task to prove this universal measure in the whole animal world. But now I formulated the gastrula theory in 1874, and afterwards (1875) reduced all the various forms of segmentation and gastrulation to one fundamental type, their meaning may be said to have been established. We have thus measured the law of unity which governs the first embryonic processes in all the animals.

Man is like all the other higher animals, especially the apes, in regard to these earliest and most important processes. As the human embryo does not necessarily differ, even at a much later stage of development—when we already perceive the cerebral vesicle, the eye, ear, gill-slots, etc.—from the similar forms of the other higher mammals, we may confidently assume that they agree in the earliest embryonic processes, segmentation and the formation of primitive layers. This has not yet, it is true, been established by observation. We have, however, had occasion to discuss a very interesting affair, investigation and discussion the movement of the segmental-cells in her embryo. However, in the earliest human embryo we have observed, and the later and more developed forms, agree with those of the whale, dog and other higher mammals, as numerous men will testify, that the segmentation and formation of layers in the eggs is laid down.

But the special form of segmentation and layer formation which we find in man is by no means the original, the primary form. It has been

derived by a very complex adaptation to embryonic condition. We cannot, therefore, understand it altogether in itself. In order to do this, we have to make a comparative study of segmentation and layer-formation in the animal world; and we have especially to make the analogies清楚 from which the animal congruity (the p. of form) has gradually been developed.

This original undivided form of segmentation and layer-formation is found today in only one case in the vertebrates, to which man belongs—the lowest and oldest member of the stem, the benthic lamprey or amphioxus (of Chapters XVI and XVII). But we find a perfectly similar gastrula-form of embryonic development in the case of many of the invertebrate animals, i.e., for instance, the annelids, brachiopods, the cephalopods (*Lamellibranchia*), the green-algae (*Chlorophyceae*) and many of the echinoderms and coelenterates, such as the ascidians, tunicates and sea-urchins, many of the molluscs and corals, and the simplest species of *Ctenophores*. We may take in an illustration the gastrula-metamorphosis in an egg-field animal world, which I observed at the Red Sea, and denoted as *Mesoneurus*.

The unsegmented mass of the egg (Fig. 1, A) first splits into two equal cells (A). Then, the nucleus of the second and its several body-shells are resorbed. These result from rapid cell-division, and not as varieties of migration on the surrounding protoplasm, as suppose of this, the protoplasm is surrounded by a cellular barrier, and, in turn, divides into two halves. Each of the two segmental-cells then penetrates what is the same way into the equal cells. The four segmental-cells (grand-daughters of the stem-cell) lie in the places. Now, however, each of them subdivides into two equal halves, the division of the surface again proceeding that of the surrounding protoplasm. The eight cells which thus arise break into sixteen, these into thirty-two, and these (each subsequently divided) into sixty-four, 128, &c. The final result of this

\* The reader of *Segmentation and Layer-Formation* will find a detailed description of the process of segmentation in a lamprey-embryo, and also the details of the formation of the primary layers in the same, in the first chapter of the present work.

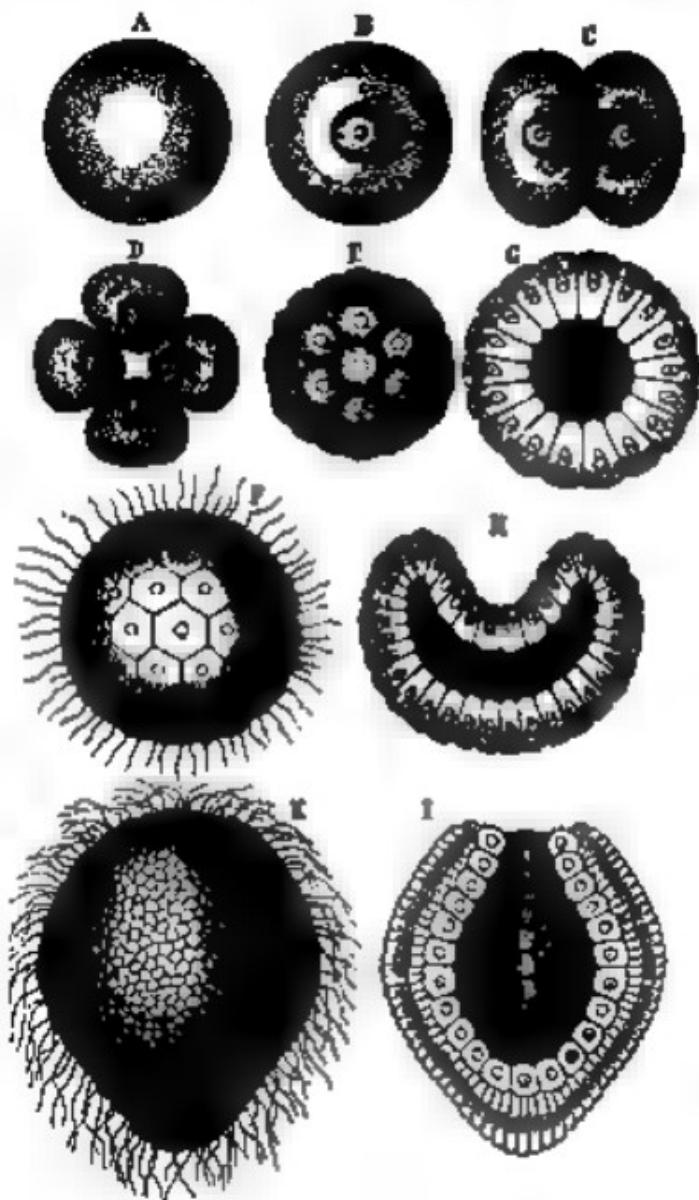


Fig. 7.—Gastrulation of a ctenophore embryo. A, B, Monocyte (young or unsegmented egg). C, A two-cell stage (the monocyte has divided). D, E, F, G, H, I, J, K, Gastrula (hexagonal), Gastrula (circular), Gastrula (irregular).

isolated elements in the formation of a cellular cluster of similar segmentation cells, which we call the *endodermoblasts*, or *mesoblasts*. These cells are usually joined together like the parts of a jelly-egg or blackberry, and this gives a happy appearance to the surface of the embryo (Fig. 5).

When the cleavage is thus ended, the embryo has massed upon it a hollow globular sphere. Within this or jelly-sphere reside the germinative cells, the segmentation-cells are banished, and all run to the surface. There they are absorbed by the endoplasma, and arrange themselves side by side in one regular layer (Figs. 5, 6). This layer of cells is called the *germinative membrane* (or *Mesoblasten*). The *mesoblasten*-cells which compose the simple structure are called the *mesoblasten-cells*; and the whole hollow sphere, the walls of which are made of the preceding, is called the *Mesoblast* or *Mesosphere*.

In the case of our own, and of many other lower forms of animal life, the young embryo begins its course to move independently and even about in the water. A thin, long, thread-like process, a sort of tail or limb, grows out of each *mesoblasten*-cell, and these independently directed, vibratory movements, move at first, but quickly after a time (Fig. 7) the tiny and *mesoblasten*-cell becomes a distinct cell. The combined force of all these vibratory bodies causes the whole Mesoblast to move about in a vibratory motion. In many other animals, especially those in which the embryo develops within certain membranes, the vibratory cells are only formed at a later stage, or even not formed at all. The *mesoblasten*-cells set the surface of the sphere vibratory and increasing, and soon find a receptacle in the internal cavity. There are still today some organisms that remain throughout life at the vibratory stage of the Mesoblast—either mobile and under direct influence of a vibratory movement in the water.

The vibratory cells that make up the body of the embryo develop gradually to a greater size, and to greater and greater numbers, until finally they are so great that their vibrations affect the whole sphere, and cause it to move about. The result of this is that the vibratory cells, which were at first scattered over the entire surface of the sphere, now form a central mass, and the rest of the surface is covered with a thin, thin skin, or envelope. This envelope is called the *ectoderm*, and the central mass of vibratory cells is called the *mesoderm*.

the wall of which is composed of a single layer of cells, such as the valves, the *mesophores*, *gutters*, etc. We shall speak further of the great physiological significance of this fact in the *mesoblast* Chapter.

A very important and remarkable process now follows—namely, the moving or migration of the Mesoblast (Fig. 8). The whole with a single layer of cells becomes preserved into a cap with a wall of two layers of cells (cf. Figs. 6, 8, 11). A certain spot at the surface of the sphere is flattened, and there blood appears. This depression, wider, deeper, and deeper, spreading as the rest of the internal cavity. The latter disappears as the latter deepens. At last the *mesoblast* rapidly disappears through the larger side of the *mesosphere* (that which bears the depressions owing to the blood on the outer side). At this time all the cells of the two surfaces assume different sizes and shapes, the inner cells are more rounded and the outer more oval (Fig. 9). In this way the embryo takes the form of a cap or pot-shaped body, with a wall made up of two layers of cells, the larger cavity of which turns to the outside at one end (the spot where the depression was originally formed). We call this very important and interesting embryonic form the "cystoblast" or "capula." (quadrat.) Fig. 9. I longitudinal section, & external view. I have in my *Natural History of Ciliates* given the name of *depot* to the remarkable intermediate body which appears at the passage of the Mesoblast into the gastrula. In the intermediate stage there are two ovaries in the embryo—the original ovary (Mesoblast) which undergoes division, and the primitive gonad (cystoblast) which is forming.

I regard the gastrula as the most important and significant embryo-form in the animal world. In all real animals that is, including the monads, just before the separation of the two portions either a pure, negative, paleogenetic gastrula (Fig. 10, 11) or an equally pure, positive, ectogenetic form, which has been developed in time from the first, and can be directly reduced to it. It is certainly a fact of the greatest interest and importance that animals of the most different sorts—vertebrates and invertebrates, molluscs and arthropods, echinoderms and annelids, radiates and spiracles, from one end the more complex the form. In *Stentor* I give a sim-

true gastrula forms from various groups of animals (Figs. 30-35, explanations given below each).

In view of this extraordinary significance of the gastrula, we must make a very careful study of its original structure. At a rate, the typical gastrula is very small, being invisible to the naked eye, or

half round, or even almost round, and is often lengthened out, or almost cylindrical.

I give the stages of primitive gut (*proto-gut*) and primitive mouth (*proto-mouth*) in the internal cavity of the gastrula-body and its opening, because this cavity is the first rudiment of the digestive cavity of

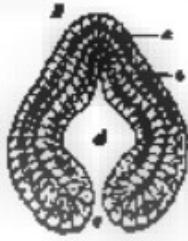


Fig. 30.



Fig. 31.

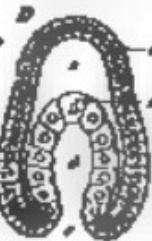


Fig. 32.

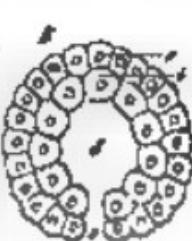


Fig. 33.

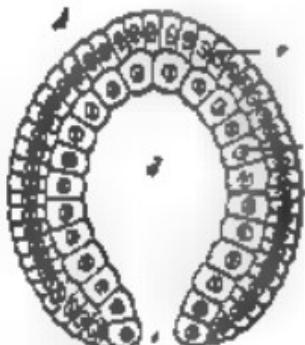


Fig. 34.



Fig. 35.

Fig. 30/35.—Gastrula of a very simple primitive-gut animal or gastrula (Gymnophyllum) (Marshall).

Fig. 31 (A).—Gastrula of a worm (Spirula). (From Marshall.)

Fig. 31 (B).—Gastrula of the ctenophores (comb-lobes, Ctenophora), not completely folded in (Annelida). (From Marshall.)

Fig. 32 (A).—Gastrula of the annelids (segmented worms). (From Marshall.)

Fig. 32 (B).—Gastrula of a mollusc (gastropod). (From Marshall.)

Fig. 33 (A).—Gastrula of a vertebrate (fish). (From Marshall.) (From Marshall's "First note.")

See much larger in the primitive-gut theory, a primitive mouth, a gastrula-animal, a gastrula-animal, a vertebrate (gymnophyllum).

at the most only visible as a fine point under very favourable conditions, and measuring generally  $\frac{1}{10}$  to  $\frac{1}{5}$  of an inch (less frequently  $\frac{1}{4}$  inch, or even more) in diameter. In shape it is usually like a roundish drinking-cup. Sometimes it is rather oval, at other times more elongated or spindle-shaped; in some cases it is

the opposite, and the opening originally serving to take food into it. Naturally, the primitive gut and mouth change very considerably afterwards in the various classes of animals. In most of the coelenterates and many of the annelids (worm-like animals) they remain unchanged throughout life. But in most of the

higher animals, and as in the vertebrates, only the larger central part of the later alimentary canal develops from the primitive gut, the later mouth is a local development, the primitive mouth disappearing or changing into the new. We must therefore distinguish carefully between the primitive gut and mouth of the gastrula and the later alimentary canal and mouth of the fully developed vertebrate.<sup>4</sup>

The two layers of cells which line the gut-cavity and comprise its wall are of extreme importance. These two layers, which are the sole builders of the whole organism, are no other than the two primary germinal layers, or the primitive

all the metazoa or multicellular animals. The skin-layer forms the external skin, the gut-layer forms the internal skin or lining of the body. Between these two germinal layers are afterwards developed the middle germinal layer (*mesoderm*) and the body-cavity (*coelome*) filled with blood or lymph.

The two primary germinal layers were first distinguished by Pander in 1817 in the *teleost* chick. Twenty years later (1837) Mantley pointed out that in many of the lower invertebrates, especially the medusae, the whole body consists throughout life of these two primary germinal layers. Soon afterwards (1853) Allman introduced the names which have come

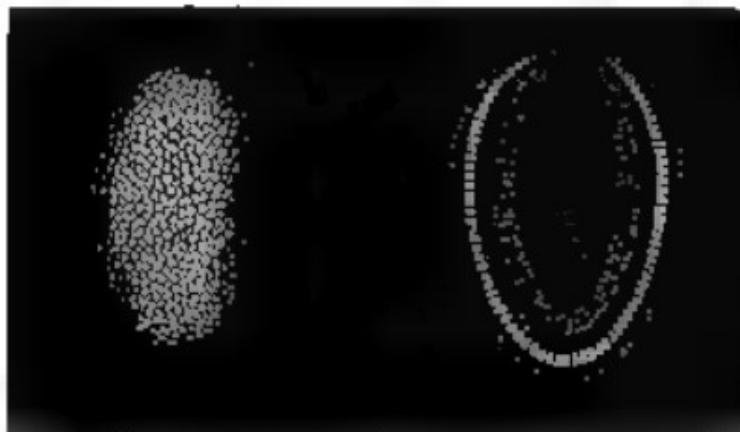


FIG. 51.—Diagram of a larva sponge (*Calyptella*). A longitudinal section through the body of a hydrorhizoid larva; a. ectoderm; mesoglea; c. mesenteron; coelome; e. choanocytes; f. endoderm layer; g. ectoderm layer; h. mesoglea; i. hypodermis.

germ-layers. I have spoken in the introductory section (Chapter III.) of their radical importance. The outer stratum is the skin-layer, or *ectoderm* (Figs. 30-33 e); the inner stratum is the gut-layer, or *endoderm* (i). The former is often also called the ectoblast, or epiblast, and the latter the endoblast, or hypoblast. From these two primary germinal layers alone is developed the entire organism of

multicellular life; he called the outer layer the *ectoderm* ("outer-skin"), and the inner the *endoderm* ("inner-skin"). But in 1851 it was shown, particularly by Kovalevsky, from comparative observation, that even in invertebrates, also, of the most different classes—annelids, molluscs, echinoderms, and articulates—the body is developed out of the same two primary layers. Finally, I discovered them (1851) in the lowest tissue-forming animals, the sponges, and proved in my Gastrula theory that these two layers must be regarded as identical throughout the animal world, from the sponges and corals, cnidaria and vertebrates, including the *annelids*, "homology

<sup>4</sup> My distinction (1851) between the primitive gut and mouth and the later permanent stomach/food-cavity and mouth (medusæ) has been much contested, but it is as much justified as the distinction between the ectoderm layer and the endoderm layer. See E. R. Lankester, *Journal of Anatomy*, Vol.

[identity] of the primary germinal layers and the primitive gut," has been confirmed during the last thirty years by the careful research of many able observers, and is now pretty generally admitted for the whole of the metazoa.

As a rule, the cells which compose the two primary germinal layers show apposition ("

stage. Generally (if not always) the cells of the skin-layer or ectoderm (Figs. 34c, 37c) are the smaller, more numerous,

layer, or entoderm ("s"), are larger, less numerous, and darker. The protoplasm of the ectodermic (outer) cells is clearer

matter of the entodermic (inner) cells, the latter are, as a rule, much richer in cell-granules (albino and fat-particles) than the former. Also the cells of the ground-layer have, as a rule, a stronger affinity for colouring matter and take on a tinge in a solution of carmine, aniline, etc., more quickly and apparently than the cells of the skin-layer. The nuclei of the entoderm-cells are usually rounded, while those of the ectoderm-cells are oval.

When the doubling-process is complete, very striking histological differences between the cells of the two layers are found (Fig. 37). The tiny, light-ectoderm-cells ("c") are sharply distinguished from the larger and darker entoderm-cells ("s"). Frequently this differentiation of the cell-forms sets in at a very early stage, during

turn appears also in the histula.

We have, up to the present, observed that form of segmented gastrulation which, for many and weighty reasons, we may regard as the original, primordial, or paleogenetic form. We

now turn to the

resemblance to each other at first (and often until the formation of the blasto-ectoderm). We give the name of the "ball-gastrula," or *embryostele*, to the gastrula that succeeds it. In just the same way (Fig. 39), we find it

lowest coelomata (the *coelenterophytes*, Fig. 30), and the simplest sponges (Spongines, Fig. 36); also in many of the medusae and hydromedusae, lower types of worms of various classes (brachiopods, nemerines, Fig. 31), tunicates (ascidians), many of the echinoderms (Fig. 32), lower articulate (Fig. 33), and molluscs (Fig. 34, and,

finally, in a slightly modified form, in the lowest vertebrates (the amphioxus, Fig. 35).

The gastrulation of the amphioxus is especially interesting because this lowest and oldest of all the vertebrates is of the highest significance in con-

nection with the vertebrate stem, a

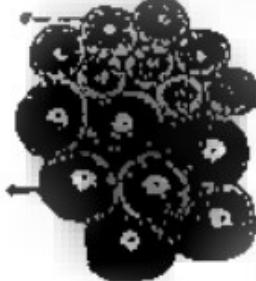
Chapter XVI. and XVII.). Just as the comparative anatomist traces the most elaborate features in the structures of the

vertebrates to divergent

development from this simple primitive

ancestor, so "secondary forms" of

formation of the germinal layers in the



amphioxus. Although this form

differs greatly from the ontogenetic models

here be regarded as paleogenetic, it nevertheless differs in some features from the quite primitive gastrulation such as we have, for instance, in the *Mesozoa* (Fig. 34) and the *Spongines*. Haeckel rightly observes that the segmentation of the ovum in the amphioxus is not strictly equal, but almost equal, and approaches the unequal. The difference in size between the two groups of cells continues to be very noticeable in the further course of the segmentation; the smaller animal cells of the upper hemisphere divide more quickly than the larger vegetal cells of the (Fig. 36 A, B). Her

blastoderm, which forms the single-layer wall of the globular Blastula at the end of the cleavage-process, does not consist of

homogeneous cells of equal size, as in the Segalids and the *Mesostomids; the cells of the upper half of the blastoderm [the mother-cells of the ectoderm] are more numerous and smaller, and the cells of the lower half [the mother-cells of the endoderm] less numerous and larger. Moreover, the segmentation-cavity of the blastula (Fig. 3, C, A) is not quite globular, but bears a horizontal spherule with unequal poles of its vertical axis. While the blastula is being folded into a cap at the vegetal pole of its axis, the difference in the size of the homogeneous cells increases (Fig. 3, D, E); it is more conspicuous when the folding has been completed and the segmentation*

has blotted down (or the increase of the cells) being greater on one side than on the other; the side that grows more quickly, and so is more curved (Fig. 3, F), will be the anterior or belly-side, the opposite, flatter side will form the back (d). The primitive mouth, which at first, in the typical archigastria, lay at the vegetal pole of the main axis, is forced away to the dorsal side; and whereas its two lips lay at first in a plane at right angles to the chief axis, they are now so far thrust aside that their plane cuts the axis at a sharp angle. The dorsal lip therefore lies the upper and more forward, the ventral the lower and hinder. In the latter, at the ventral passage of the ectoderm into the endoderm, there lie side by side a pair of very large cells, one to the right and one to the left (Fig. 3, F); these are the important polar cells of the primitive mouth, or "the primitive cells of the mesoderm." In consequence of these considerable cellular actions taking in the course of the gastrulation, the primitive unsegmented form of the archigastria in the amphibia has already become divided, and thus the head-and-trunk, or dorsal-anterior, or the ventral-posterior body has already been determined.

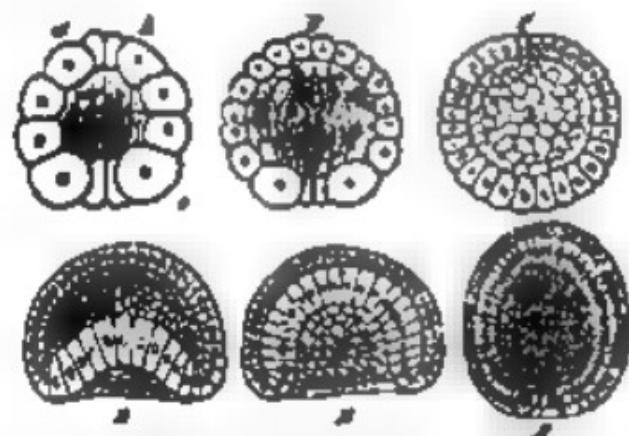


FIG. 3.—Diagrammes of the amphibia, from Haeckel's *Fundamentals of Zoology*, 2nd ed., 1895. A, B, C, D, E, F, early stages in the formation of the head and trunk; M, N, O, P, Q, R, S, T, U, V, W, X, Y, Z, later stages in the formation of the body, showing a definite gastrulation.

blastopore (Fig. 3, F). The larger vegetal cells of the ectoderm are thicker at gastrulation, and so darker than the smaller and lighter animal cells of the endoderm.

But the unequal gastrulation of the amphibia diverges from the typical equal division of the Segalids, the *Mesostomids* (Fig. 2), and the *Ophiostomes* (Fig. 3, B), in another important particular. The pure archigastria of the latter forms is uniform, and it is round in its whole length in transverse section. The vegetal pole of the vertical axis is just in the cavity of the primitive mouth. This is not the case in the gastrula of the amphibia. During the folding of the blastula the dorsal axis is already bent on one side, the growth of

This has been transmitted by amphibia to all the other modified gastrula-forms of the vertebrate stem.

Apart from this bilateral structure, the gastrulae of the amphibia resemble the typical archigastria of the lower animals (Figs. 3, 4, 5) in developing that two primary germinal layers form a single layer of cells. This is clearly the oldest and original form of the metazoic embryo. Although the animals I have mentioned belong to the most diverse classes, they nevertheless agree with each other, and many more animal forms, in having retained to the present day, by a conservative faculty, this prehistoric form of gastrulation which they have from their

earliest common ancestors. But this is not the case with the great majority of the animals. With these the original embryonic process has been gradually less altered in the course of

the course of time, so that it can clearly be distinguished from the formative process. As a rule, the formative-yolk (with the gastrulae vesicle) then usually gathers at one pole and the food-yolk at the other. The first is the *animal*, and the second the *vegetal*, pole of the

segmentation of the ovum and the subsequent gastrulation have in this way been considerably changed. In fact, these variations

in the course of time

were not rightly understood in animals, and the gastrula was interpreted. It was not until I had made an extensive comparative study, holding a considerable sum (for the years 1866-73), in animals of the most diverse classes, that I succeeded in showing the same common typical process in these apparently very different forms of gastrulation, and tracing them all to one original form. I repeat all those that diverge from the primary palindromic gastrulation as secondary, modified, and degenerate. The more or less divergent form of gastrula that is produced may be called a secondary, modified gastrula, or a *metagastula*. The reader will find a scheme of these different kinds of segmenting-gastrulation at the close of this paper.

By far the most important process that determines the various embryogenetic forms of gastrulation is the change in the nutrition of the ovum and the accumulation in it of nutritive yolk. By this we understand various chemical substances (chiefly granules of albumen and fat-particles) which serve exclusively as reservoirs of food for the embryo. As the metazoic embryo in its earlier stages of development obtains its food and to build up the tissues, the necessary material has to be taken up in the ovum. Hence we distinguish in the ovum two chief elements—the active formative-yolk (protoplasm) and the passive food-yolk (cytoplasma, wrongly spoken of as "the yolk"). In the little palindromic ova, the segmentation of which we have already considered, the yolk-granules are so small and irregularly distributed in the protoplasm of the ovum that the even and repeated cleavage is not affected by them. But in the great majority of the animal ova the food-yolk is more or less considerable, and is stored in a certain part of the ovum, so that even in the unfertilized ovum the "granular"

ova (*"infertilized"* ova, or ova with the yolk at one end [*tertio rotundum* in the cyclostomes and amphibia]), the gastrula-

way that in the cleavage of the impregnated ovum the animal (usually the upper) half splits up more quickly than the vegetal (lower). The contractions of the active protoplasm, which effect this continual cleavage of the cells, meet a greater resistance in the lower vegetal half from the passive cytoplasm than in the upper animal half. Hence we find in the latter



Fig. 2.—Micrograph of the unfertilized ovum from *Amphioxus* (from *Die Naturgeschichte der Tiere* by H. Müller, 1870).

more large, and in the former fewer and larger, cells. The animal cells pro-

duce the external, gastrinal layer.

Although this unequal segmentation of the cyclostomes, gnathostomes, and amphibia seems at first sight to differ from the original equal segmentation (for instance, in the monostomids, Fig. 19), they both have this in common, that the cleavage process throughout affects the whole cell. Hence Kowalev called it *total segmentation*, and the ovum in question holoblastic, or "whole-cleaving." It is otherwise with the second chief group of ova, which distinguish themselves as *ectoblastic*, or "externally-cleaving": to this class belong the familiar large eggs of birds and reptiles, and of most fishes. The last name of the passive food-yolk is ap-

large in those cases that the protoplasmic migration of the native cells cannot affect any further changes. In consequence, there is only a partial regeneration. While the protoplasmic action of the ovum continues infinity to divide, multiplying the people, the destruction in the vegetal series remains more or less undivided, it is entirely controlled as fixed by the forming cells. The larger the accumulation of food, the more restricted is the process of regeneration. It may, however, continue for some time even after the gastrulation is more or less complete. In the cases that the vegetal cellular division in the gastrulae slowly ceases by cleavage; no death of them is accompanied by a small quantity of protoplasm. It may afterwards appropriate a portion of the food-yolk, and then form a new "embryo" of memory. When this vegetal differentiation continues for a long time, after the two primary germinal layers have been formed, it forms the basis of the "after-gastrulation."

The meroblastic ova are only found in the larger and more highly developed vertebrates, and only in them a few embryos make a longer time and on less materials than in the local regeneration. According to the yolk-food accumulation at the centre of the side of the ovule, we distinguish two groups of developing ova, parthenogenetic and diembryonic. In the parthenogenetic the food-yolk is in the centre, enclosed inside the ovule (hence they are also called "centralized" ova); the forming cells surround the food-yolk, and so suffice itself a superficial cleavage. This is found among the arachnidiforms, spiders, insects, etc.; in the diembryonic ova the food-yolk gathers at one side, at the vegetal or lower pole of the central axis, while the nucleus of the ovule and the great bulk of the nutritive yolk lie at the upper or animal pole (hence these ova will also called "animalized"). In these cases the cleavage of the ovum begins at the upper pole, and leads to the formation of a dorsal shield embryo. This is the case with all meroblastic vertebrates, most fishes, all reptiles and birds, and the higher mammals (the mammals).

The gastrulation of the diembryonic ova, which chiefly concern us, often leads to microscopical observations and photomicrography. These, however, have been rendered by

the comparative embryological researches has been conducted by a number of distinguished observers during the last few decades—especially the brothers Hertwig, Raik, Kugler, Blaschka, Ruckerl, Gause, Reuter, etc. These thorough and careful studies, aided by the most perfect modern improvements in mechanical methods (by staining and dissection), have given a very welcome support to the views which I put forward in my work, *On the Gastrula and the Regeneration of the Animal Organ* (see translation), as follows. As it is very important to understand than others and their physiognomy清楚ly, not only in regards evolution in general, but particularly in connection with the process of man, I will give here a brief statement of them as far as they concern the gastrulation.

1. All the vertebrates, studied up now, are physiologically (or gastronomically) related—that is, the members of one single natural class.

2. Consequently, the embryonic processes in these multicellular development stand side by side in a general connection.

3. As the gastrulation of the vertebrates shows the simplest features, that of the other vertebrates must have been derived from it.

4. The comparative studies now of the latter are still applicable since hardly is stored up in the earth.

5. Although the size of the food-yolk may be very large in the case of the dicamptodonts, etc., yet it is in every case a Mosaic to develop from the ovaries, as in the holothurians, etc.

6. And, in every case, the gastrula develops from the blastula by cutting off a segment.

7. The cavity which is produced in the latter, by this cutting is, in each case, the primitive gut (proto-intestine), and no opening the primitive mouth (proto-anus).

8. The food-yolk, whether large or small, is always placed in the ventral wall of the primitive gut; the cells (called "archenteron") which may be formed in a subsequently (by "after-gastrulation") also belong to the lower germinal layer, like the cells which immediately enclose the primitive gut-walls.

9. The primitive mouth, which is built in below at the lower pole of the ventral axis, is formed by the growth of the yolk, backwards and thus opens

towards the dorsal side of the embryo; the ventral axis of the primitive gut is thus gradually converted into horizontal.

3. The primitive mouth is closed sooner or later in all the vertebrates, and does not evolve into the permanent mouth-aperture; it rather corresponds to the "prostomium," or region of the gut. From this important point the formation of the middle germinal layer proceeds, between the two primary layers.

The wide comparative studies of the invertebrates I have named have further shown that in the case of the dissimilate higher vertebrates (the three classes of mammals, the primitive mouth of the amniotes, etc., which are being looked for at once), it is found always, and is nothing else than the familiar "prostomium." Of this we shall say more in the present chapter. Moreover we realize that gastrulation still is required to one and the same process in all the vertebrates. Moreover, the various forms of life in the invertebrates are always to be referred to one of the four types of segmentation described above. In relation to the distinction between oral and vegetal segmentation, the grouping of the various forms is as follows:

1. Vertebrates (Amphibia, Mammalia) Invertebrates (Diplopoda, Crustacea, Mollusca, Annelida)	<div style="display: flex; justify-content: space-around;"> <div style="text-align: center;"> <b>Figurative</b> Metamorphosis Development</div> <div style="text-align: center;"> <b>Testicell</b> Metamorphosis Development Vegetation</div> </div>
2. Ciliates & Rd. Organisms Type Developed in Endosoma	<div style="display: flex; justify-content: space-around;"> <div style="text-align: center;"> <b>Figurative</b> Metamorphosis Development Vegetation</div> <div style="text-align: center;"> <b>Testicell</b> Metamorphosis Development Vegetation</div> </div>

The lower animals we know—namely, the heteromorphous (amoebae, simple polyps, etc.)—remain throughout life at a stage of development which differs little from the gastrula; their whole body consists of two layers of cells. This is a fact of extreme importance. We see that man, and also other vertebrates, pass quickly through a stage of development in which they consist of two layers, just as these lower animals do throughout life. If we apply our biogeographic law to the matter, we at once reach this important conclusion: "Man and all the other animals which pass through the two-layer stage,

or gastrula-stage, in the course of their embryonic development, must descend from a primitive simple two-layer, the whole body of which consisted throughout life (as is the case with the lower amphineurotes), namely of two cell-layers or primary layers. We will call this primitive two-layer, with which we shall deal more fully later on, the gastrula—that is to say, "gastrula-gut animal."

According to this gastrula-theory there was originally in all the multicellular animals no organ with the same structure and function. Thus was the primitive gut; and the two primary germinal layers which form its wall must also be regarded as identical in all. This organic homogeneity or identity of the primary germinal layers is proved, on the one hand, from the fact that the gastrula was originally formed in the same way in all forms—namely, by the covering of the mesoblast; and, on the other hand, by the fact that in every case the same fundamental organs arise from the germinal layers. The outer or animal layer, or ectoderm, always forms the outer organs of animal life—the skin, nervous system, cerebrospinal, etc., the outer or vegetal layer, or endoderm, gives rise to the chief organs of vegetative life—the organs of respiration, digestion, blood-formation, etc.

In the lower amphibians, whose body remains at the two-layer stage throughout life, the gastrula, the simple amphibians (Cyclostomes), and polyzoa (*Hildenia*), these two groups of functions, animal and vegetal, are strictly divided between the two simple primary layers. Throughout life the outer or animal layer acts simply as a covering for the body, and accomplishes its movement and nutrition. The inner or vegetative layer of cells acts throughout life as a giving-off, or nutritive layer of ectocytic cells, and often also as the reproductive cells.

The last form of these "gastrotoids," or "gastrula-like animals," is the common land-worm (of *Hildenia*). This amphibian of all the chordomorphs, it is true, a crowd of tentacles round its mouth. Also its outer gastrular layer has certain special modifications. But these are secondary additions, and the inner gastrular layer is a simple structure of cells. On the whole, this body has preserved to our day by hereditarily the simple structure of our primitive amphibia, the gastrula (cf. Chapter XIII.).

## THE GASTRULA THEORY

In all other animals, particularly the vertebrates, the gastrula is merely a brief transitional stage. Here the two-layer stage of the embryonic development is quickly succeeded by a three-layer, then four-layer, stage. With

appearance of the four superimposed germinal layers we reach again a form and steady starting-ground, from which we may follow the further, and much more difficult and complicated, course of embryonic development.

### SUMMARY OF THE CHIEF DIFFERENCES IN THE OVUM-SEGMENTATION AND GASTRULATION OF ANIMALS.

The animal names are referred to the letter sign: *e* Zoophytes, *d* Annelids, *r* Molluscs,  
*f* Echinoderms, *s* Invertebrates, *t* Thuringia, *c* Vertebrates.

<b>Indirect oviparous</b> <i>Amphioxus</i>	<b>I. External segmentation.</b> <i>Amphioxus</i>	<b>II. Internal segmentation.</b> <i>Amphioxus et al.</i>
<b>Direct oviparous.</b> <i>Amphioxus</i>	<b>III. External segmentation.</b> <i>Amphioxus et al.</i>	{ <i>Cyclostomes et cetera.</i> <i>Amphioxus et cetera.</i>
<b>Gastrula with mesoglea and yolk.</b> <i>Amphioxus</i>	<b>IV. External segmentation.</b> <i>Amphioxus et al.</i>	{ <i>Prostomes, Ciliates, Ascidians, Echinoderms,</i> <i>Amphioxus et cetera.</i>

## THE GASTRULATION OF THE VERTEBRATE<sup>1</sup>

The remarkable processes of gastrulation, ovum-segmentation, and formation of germinal layers present a most conspicuous variety. There is to-day only the larva of the vertebrates, the amphioxus, that exhibits the original form of these processes, or the palaeogenetic gastrulation which we have considered in the preceding chapter, and which culminates in the formation of the archegonial (Fig. 38). In all other extant vertebrates these fundamental processes have been more or less modified by adaptation to the conditions of embryonic development (especially by changes in the food-pellet). They exhibit various categories of types of the formation of germinal layers. However, the different classes vary considerably from each other. In order to grasp the unity that underlies the manifold phenomena and

the unity of the  
phylogeny

"unity," which I developed in my *General Morphology* in 1866, is now generally accepted. All impartial zoologists agree to-day that all the vertebrates, from

and the fishes to the ape and

man, descend from the primitive vertebrates.<sup>2</sup> Hence the embryonic processes, by which each individual vertebrate is developed, must also be capable of being reduced to one common type of embryonic development; and this primitive type is most certainly exhibited to-day by the amphioxus.

It must, therefore, be our next task to make a comparative study of the various forms of vertebrate gastrulation, and trace them backwards to that of the larva. Broadly speaking, they fall first into two groups: the older cyclostomes, the earliest fishes, most of the amphibia, and the viviparous mammals, have de-

veloped one—that is to say, one with total, complete segmentation; while the younger cyclostomes, most of the fishes, the cephalopoda, reptiles, birds, and monotremes, have metamerous ova, or ova with partial discoidal segmentation. A closer study of them shows, however, that these two groups do not present a natural entity, and that the historical relations between their several divisions are very complicated. In order to understand them properly, we must first consider the various modifications of gastrulation in these classes. We may begin with that of the amphioxus.

The most suitable and most available objects of study in this class are the eggs of our indigenous amphibia, the tall frog and toad, and the tailless salamander. In spring they are to be found in clusters in every pond, and careful examination of them will show a

and features of the

in order to understand the whole process rightly and follow the formation of the germinal layers and the gastrula.

The frog and salamander must be carefully hardened; then the thinnest possible sections must be made of the hardened ova with the microtome, and the cut sections must be very closely compared under a powerful microscope.

The ova of the frog or toad are globular in shape, about the twelfth of an inch in diameter, and are clustered in jelly-like masses, which are lumped together in the case of the frog, but form long strings in the case of the toad. When we examine the opaque, grey, brown, or blackish ova closely, we find that the upper half is darker than the lower. The middle of the upper half is in many species black, while the middle of the lower half is white. In this way we get a definite axis of the ovum with two poles. To give a clear

<sup>1</sup> Cf. Haldane's *Manual of Comparative Embryology*, vol. II; Theodore Boveri's *The Development of the Frog's Egg*.

<sup>2</sup> The colouring of the eggs of the amphibia is caused by the accumulation of darkening matter at the animal pole of the ovum. In consequence of this, the upper cells of the embryo are darker than the vegetal cells of the ovule. We find the reverse of this in the case of such animals, the protoplasm of the abductor cells being usually darker and more granular.

idea of the segmentation of this ovum, it is best to compare it with a globe, on the surface of which are marked the various parallels of longitude and latitude. The superficial dividing lines between the different cells, which come from the repeated segmentation of the ovum, look like deep furrows on the surface, and hence the whole process has been given the name of furcation. In reality, however, this "furcation," which was formerly regarded as a very mysterious process, is

in this position throughout the course of the segmentation, and its cells multiply much more rapidly. Hence the cells of the lower hemisphere are found to be larger and less numerous. The cleavage of the stem-cell (Fig. 40 A) begins with the formation of a complete furrow, which starts from the north pole and reaches to the south (B). An hour later a second furrow arises in the same way, and this cuts the first at a right angle (Fig. 40 C). The ovum is thus divided into four equal

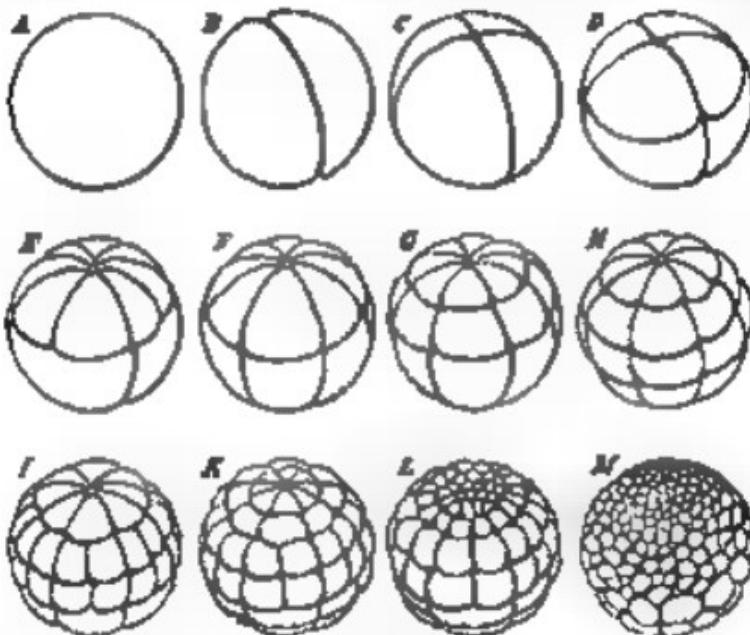


FIG. 40.—The alternation of Cleavage's stages (represented by lines). A, stem-cell; B, the first two segments; C, four cells; D, eight cells, 4 normal and 4 vegetative; E, sixteen cells (8 normal and 8 vegetative); F, thirty-two cells; G, sixty-four cells; H, one-hundred-and-twenty-eight cells; I, two-hundred-and-fifty-six cells; J, five-hundred-and-twenty-four cells; K, one-thousand-and-one-hundred-and-twenty-four cells; L, two-thousand-and-one-hundred-and-twenty-four cells; M, six-thousand-and-one-hundred-and-twenty-four cells.

nothing but the familiar, repeated cell-segmentation. Hence also the segmentation-cells which result from it are said cells.

The unequal segmentation which we observe in the ovum of the amphibia has the special feature of beginning at the upper and darker pole (the north pole of the terrestrial globe in our illustration), and slowly advancing towards the lower and brighter pole (the south pole). Also the upper and darker hemisphere contains

parts. Each of these four "segmented cells" has an upper and darker and lower, brighter half. A few hours later a third furrow appears, vertically to first two (Fig. 40 F). The globule is now composed of eight cells, four near ones above (northern) and four far ones below (southern). Next, each of the four upper cells divides again by a cleavage beginning from the pole, so that we now have eight above and four below (Fig. 40 G). Later, the

four new longitudinal divisons extend gradually to the lower cells, and the number rises from twelve to sixteen (*P*). Then a second circular furrow appears, parallel to the first, and reaches to the north pole, so that we may compare it to the north polar circle. In this way we get twenty-four segmentation-cells—sixteen upper, smaller, and darker ones, and eight smaller and brighter ones below

in succession forty, forty-eight, fifty-six, and at last sixty-four cells (*I*, *K*). In the meantime, the two hemispheres differ more and more from each other. Whereas the sluggish lower hemisphere long remains at thirty-two cells, the lively northern hemisphere quickly subdivides twice, producing first sixty-four and then still cells (*L*, *M*). Thus we reach a stage in which we count on the surface



FIG. 44.

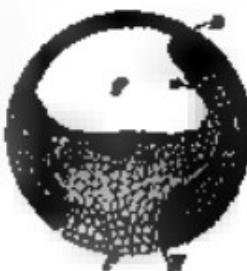


FIG. 45.



FIG.



FIG. 47.

## GROWTH OF THE EMBRYO IN FOUR STAGES

the upper half of the body, *A*, *B* ventral half, *C* dorsal half, *D* upper perspective view of the head at the upper pole, *E* yellowish part of the epiblast (Koch's "germinal epithelium"). *F* a groove just over the hypoblast or micromere (micromeric depression). The primitive mouth (prostomium) is closed by the polythorax; *G* a partition between the primitive gut cavity (*H*) and the segmentation cavity (*I*, *J*, *K* anterior of the large coelomic hypoblast of the primitive mouth (the hypocoelous angle). The line of dots between *G* and *H* indicates the future connection of the polythorax (*I*) with the central mass of the yolk-sac (*K*). Note that on the one hand the yolk-sac is turned out so that the back of the embryo is uppermost and the ventral side down. (See Structure.)

(*G*). Soon, however, the latter also subdivide into sixteen, a third of "meridians of latitude" appearing, this time in the southern hemisphere; this makes thirty-two cells altogether (*H*). Then eight new longitudinal lines are formed at the north pole, and these proceed to divide, first the darker cells above and afterwards the lighter southern cells, and finally reach the south pole. In this way we get

of the same cell wall cells in the upper half and thirty-two large ones in the lower half, or 64 altogether. The dissimilarity of the two halves increases: while the northern breaks up into a great number of small cells, the southern consists of a much smaller number of larger cells. Finally, the dark cells of the upper half grow almost over the surface of the ovum, leaving only a small circular spot

at the south pole, where the large & cells of the lower half are visible. This white region at the south pole corresponds, as we shall see afterwards, to the primitive mouth of the gastrula. The

most important part of the embryo (Fig. 41 & 42). Soon the primitive gut-cavity stretches further and further at the expense of the segmentation-cavity ( $P$ ), until at last the latter disappears altogether. The two cavities are only separated by a thin partition (Fig. 43 a). With the formation of the primitive gut our frog-embryo has reached the gastrula stage, though it is clear that this congeneric amphioxus gastrula is very different from the real paleogenetic gastrula we have considered (Figs. 30-36).

In the growth of this hooded gastrula we cannot sharply mark off the various stages which we distinguish successively between blastula and gastrula. Nevertheless, it is not difficult to realize the whole congeneric or disturbed development of the amphigastula to the true paleogenetic formation of the archigasterite of the amphioxus.

This reduction becomes weaker if, after considering the gastrulation of the tallest amphibia (frog and toad), we glance for a moment at that of the tallest amphibia, the urodeles. In some of the latter, that have only recently been carefully studied, and that are phylogenetically older, the process is much simpler and easier than is the case with the former and longer known. Our common salamander (*Phryne larvata*) is a particularly good subject for observation. Its primitive yolk is much smaller and its formative yolk less obscured than black pigment-cells than in the case of the frog, and its gastrulation has better retained the original paleogenetic character. It was first described by Scott and Dubois (1895), and Oscar Hertwig especially made

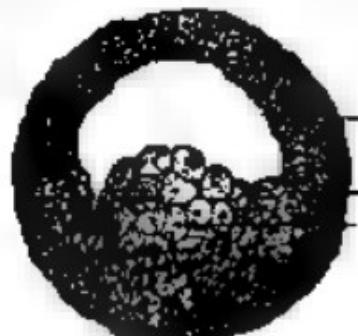


FIG. 41.—Details of the water-amphioxus (*Ampioxus*), *41*, appearance of the gastrula; *42*, later stage (from Hertwig).

of the inner and larger and clearer cells (including the white polar region) belongs to the ectoderm layer. The outer envelope of dark smaller cells forms the ectoderm or skin-layer.

In the meantime, a large cavity, full of fluid, has been formed within the globular body—the segmentation-cavity or endoderm-cavity (*Rudimentum*, Figs. 41-44 *A*). It extends considerably as the cleavage proceeds, and afterwards assumes an almost semi-circular form (Fig. 45 *A*). The frog-embryo now represents a modified embryonic vesicle or blastula, with hollow animal half and solid vegetal half.

Now a second, narrower but longer, cavity arises by a process of folding at the lower pole, and by the falling away from each other of the white ectoderm-cells (Figs. 41-44 *N*). This is the primitive gut-cavity or the gastric cavity of the gastrula, *prostomia* or *archistomia*. It was first observed in the ova of the amphibia by Ruderaria, and so called the Ruderaria cavity. The reason of its peculiar narrowing here is that it is, for the most part, full of yolk-cells of the ectoderm. These also stop up the whole of the wide opening of the yolk, and form what is known as the "yolk-stopper," which is open freely at the white round spot at the south pole ( $P$ ). Around it the ectoderm is much thicker, and forms the border of the primitive mouth, the

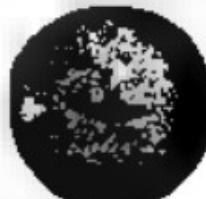


FIG. 45.—Sagittal section of frog (*Rana temporaria*), with the flattened tail of the posterior velum (from Hertwig).

archistomia. Its globular blastula (Fig. 45) is loosely aggregated, yolk-

Filled entodermic cells or yolk-cells (*dy*) in the lower vegetal half; the upper, animal half encloses the hemispherical segmentation-cavity (*sh*), the curved roof of which is formed of two or three

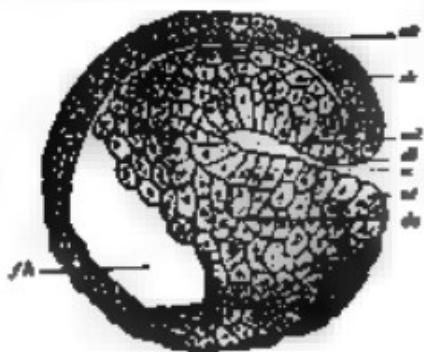


Fig. 41.—Illustrated process of a holocephalo-metameric embryo of Cephalopoda (Diagram of the commencement of gastrulation). The older vertebral larva, so called because it is surrounded by an animal segmental capsule, is represented here as a primitive mouth at first at dorsal, and secondly near the mouth of a teleost. (From Herreng.)

have the 'border zone' (*zo*). The folding which leads to the formation of the gut-tube takes place at a spot in this border zone, the primitive mouth (Fig. 46 a).

Unequal segmentation takes place in some of the cyclostomes and in the older fishes in just the same way as in most of the amphibia. Among the cyclostomes ("round-mouthed") the lamprey is halfway between the actinopterygians

and the heterodontids.

Actinopterygians, and in them a special class of vertebrates—ovum-segmentation in our common river-lamprey (*Petromyzon herenii*) was described by Miss Schwabe in 1876, and afterwards by Scott (1883) and Goette (1890).

Unequal total segmentation follows the same lines in the older fishes, the teleosts and ganoids, which are directly derived from the cyclostomes. The primitive fishes (*Seletches*), while ancestral group of the two classes,

generally considered, until a short time ago, to be diploblastic. It was not until the beginning of the twentieth century that Masaharu Danin made the important discovery in Japan that one of the oldest living fishes of the shark type (*Cephaloscyllium jejuense*) has the same total unequal segmentation as the amphiblastic plated fishes (*ganoids*).<sup>1</sup> This is particularly interesting in connection with our subject, because the few remaining survivors of this division, which was so numerous in palaeozoic times, exhibit three different types of gastrulation. The oldest and most conservative form of the modern ganoids are the scaly sturgeons (*Sturisomata*), plated fishes of great evolutionary importance, the eggs of which are often as caviar; their cleavage is not markedly different from that of the leptocephalus and the amphibia. On the other hand, the most modern of the plated fishes, the beautifully scaled bony fishes of the North American rivers (*Lepidosteus*), approaches the osseous fishes, and is distinctive like them. A third genus (*Labeo*) is midway between the sturgeons and the latter.

The group of the lung-fishes (*Diplopeltis* or *Thyrsites*) is closely connected with the older ganoids. In respect of their whole

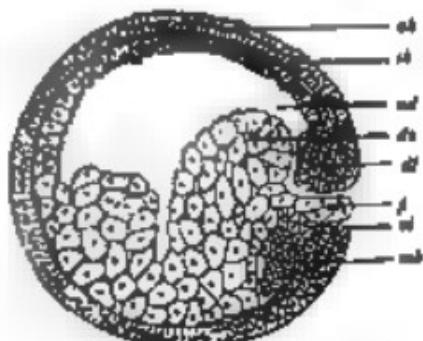


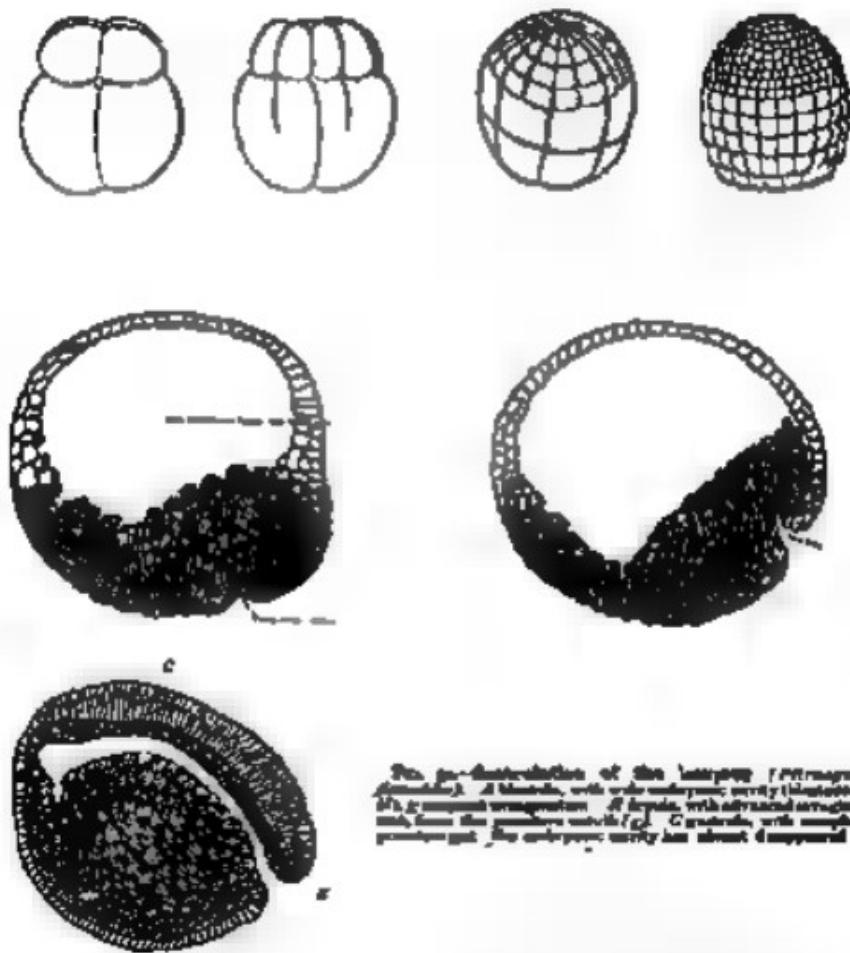
Fig. 42.—Trophoblast portion of the gastrula of the teleostean heterodontid *Frenichthys*. (From Herreng.)

organization they are midway between the gill-breathing fishes and the lung-breathing neopterygians, they share with the former the shape of the body and fins, with the latter the form of the heart.

<sup>1</sup> Masaharu Danin, Histochemical Changes in the Egg of *Cephaloscyllium jejuense* Miura. *Archiv für mikroskopische Anatomie und Physiologie*, vol. 26, 1910.

and lungs. Of the older diplopods (*Pholidoceratinae*) we have now only one specimen, the remarkable *Ceratodus* of East Australia; its amphiblastic gastrulation has been recently explained by Richard Swinnerton (cf. Chapter XXI.). That of the two

and hæmichela, belong to the old, conservative groups of our stem. Their unequal cleavage, segmentation and gastrulation have many peculiarities in detail, but can always be compared with comparative ease to the original cleavage and gastrulation



The gastrulation of the lamprey (*Petromyzon*). A. Blastula, with older underlying ventrally located germ ring. B. Gastrula, with advanced invagination and some of the surface epithelium. C. Gastrula, with complete invagination; the embryo cavity has almost completed a

America, is not materially different." (Cf. Fig. 51.)

All these amphiblastic vertebrates, Petromyzon and *Ceratodus*, *Acanthocepss* and *Ceratodus*, and also the teleostei

of the lowest vertebrate, the lampreys; and this is little removed, as we have seen, from the very simple archigastria of the *Sagittaria* and *Notopterus* (see Figs. 29-38). All these and many other classes of animals generally agree in the circumstance that in segmentation their

ovum divides into a large number of cells by repeated cleavage. All such eggs have been called, after Korschelt, "whole-dividing" (*holoblastic*), because their division is complete or total.

In a great many other classes of animals this is not the case, as we find (in the vertebrate stem) among the birds, reptiles, and most of the fishes; among the insects and most of the spiders and

of the ovum; this alone divides in segmentation, and produces the numerous cells which make up the embryo. On the other hand, the nutritive yolk is merely a passive part of the contents of the ovum, a metabolizable element which contains nutritive material (albumin, fat, etc.), and so represents in a sense the proprie-  
ties of the developing embryo. The latter takes a quantity of food out of this

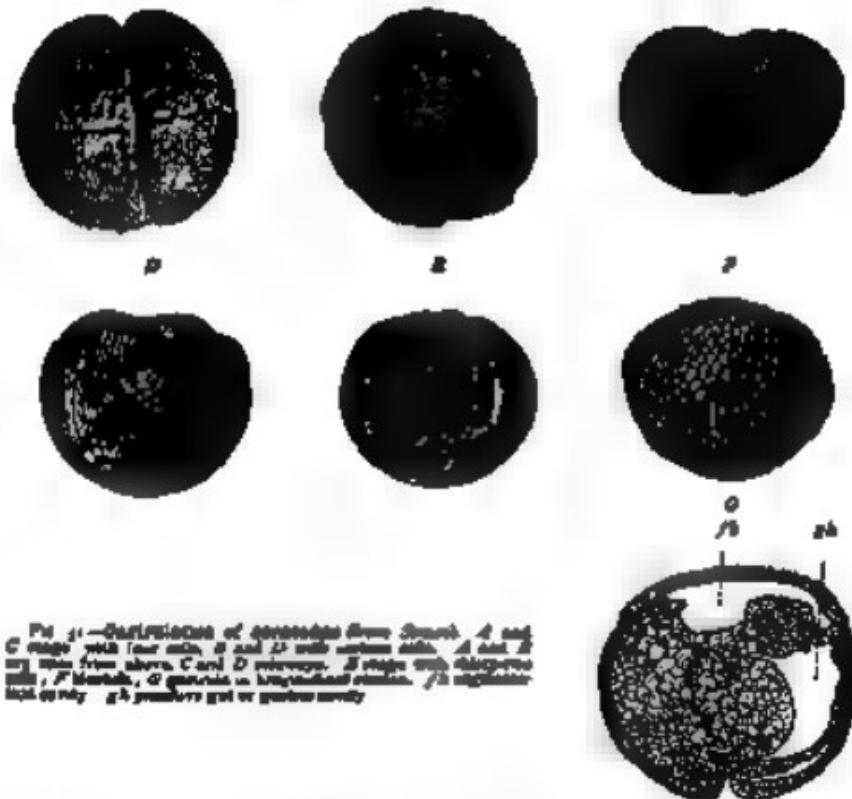


FIG. 31.—CLEAVAGES OF OVIPAROUS FISHES. A and C eggs with four cells; B and D with sixteen cells; A and B seen from above; C and D sideways; E seen with oblique light; F morula; G gastrula in longitudinal section; H yolked egg; I yolked egg with yolk cavity.

crabs (of the artiopods); and the cephalopods (of the molluscs). In all these animals the mature ovum, and the stem-cell that arises from it in fertilisation, consist of two different and separate parts, which we have called formative yolk and nutritive yolk. The formative yolk alone consists of living protoplasm, and is the active, evolutionary, and nucleated part

store, and finally consumes it all. Hence the nutritive yolk is of great indirect importance in embryonic development, though it has no direct share in it. It either does not divide at all, or only later on, and does not generally consist of cells. It is sometimes large and sometimes small, but generally many times larger than the formative yolk; and hence it is

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that it was formerly thought the more important of the two. As the respective significance of these two parts of the ovum is often strongly described, it must be a word.

real appendage. All ova that have independent nutritive yolk are called, Meitze). Their segmentation plate or partial.

There are many difficulties of understanding the part

in nucleus (*b*), this is the formative yolk of the stem-cell, or the germinal disk all fat-globule (*c*) and the

click not dividing at all; -shaped forming-yolk (*d*) proceeds quite inde-

ring these difficulties, and reducing the morphologic form of the original paleogenetic type.

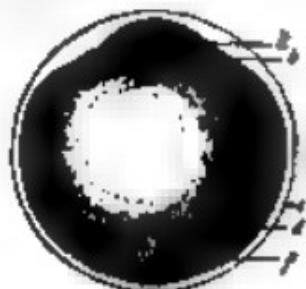


Diagram of a frog-egg body disk. After hatching of the normal *F* means of one of the globules of albumen, the nutritive cells, fat-globule, or yolk, a later substance of the ovum, is removed.

comparatively easy is the small intro-

like a "watch-glass," with thick borders (the upper and 1) of the nutritive yolk like the and the border,

turn, or a kind of turning-up of the edge of the film-cadern. In this process the segmentation-cells disappear.

The space underneath the endoderm corresponds to the primitive gut-cavity, and is filled with the decolorizing fluid-yolk (*f*). Thus the formation of the granula of our *B*-s is complete. In contrast to the two chief forms of gastrula we considered previously, we get the name of direct gastrula (theropoda, Fig. 34) to the third principal type.

Very similar to the direct gastrulation of the body-fishes is that of the lung or amphibia, the remarkable circumstances that two gastrulae in the body-cavity of fishes, and are distinguished by several notable peculiarities from their nearest

found them joined together in pairs of jolly, floating on the surface of the sea, and, as the little walls were completely

developed like those of the amphibia, the eel-like bodies out of the lung are about six inches long, and form a distinct

membrane (urodome, Fig. 34 c) to find a large, quite clear, and transparent fat-globule of albumen (*d*). At both poles of

which are situated by the large food-yolk. This takes no direct part in the

is (which is turned slow floating ova) there is a bi-layer, less composed of protoplasm, and this encloses

city of the protoplasm, controlling at the opening. If we imagine the original telo-gastrula (Figs. 30-33) trying to swallow a

ball of food which is much bigger than itself, it would spread out round it in discoid shape in the attempt, just as we find to be the case here (Fig. 53). Hence we may derive the discoid gastrula from the original ball-gastrula, through the intermediate stage of the hooded gastrula. It has arisen through the accumulation of a store of food-stuff at the vegetal pole, a "nutritive yolk" being thus formed in contrast to the "formative yolk." Nevertheless, the gastrula is formed here, as in the previous cases, by the folding or invagination of the blastoderm. We can, therefore, reduce this conogenetic form of the dorsal segmentation to the palaeogenetic form of the primitive cleavage.

This reduction is tolerably easy and confident in the case of the small ovum of our deep-sea bony fish, but it becomes

embryonic development and consumed by the embryo. This latter develops solely from the living formative yolk of the stem-cell. This is equally true of the ova of our small bony fishes and of the colossal sea of the primitive fishes, reptiles, and birds.

The gastrulation of the primitive fishes or teleosts (sharks and rays) has been carefully studied of late years by Ruckert, Röhl, and H. E. Ellinger in particular, and is very important in the sense that this group is the oldest among living fishes, and their gastrulation can be derived directly from that of the cyclostomes by the accumulation of a large quantity of food-yolk. The oldest sharks (*Catodon*) still have the unequal segmentation inherited from the cyclostomes. But while in this case, as in the case of



FIG. 53. Origin-gastrulation of a bony fish. *a*, an embryo of the teleostid *Pomacentrus*. *b*, an embryo of the teleostid *Carassius auratus*. *c*, a diagram of the gastrula of *Catodon* with a yolk-sphere, a space between the yolk-sphere and the germ, filled with protoplasm.

difficult and uncertain in the case of the large ova that we find in the majority of the other fishes and in all the reptiles and birds. In these cases the final result is, in the first place, comparatively unknown, the nutritive yolk being almost invisible beside it; and, in the second place, the yolk-yolk contains a quantity of different elements, which are known as "yellow-granules, yellow-globules, yellow-plates, yellow-filaments, yellow-villi," and so on. Frequently these definite elements in the yolk have been described as real cells, and it has been wrongly stated that a portion of the embryonic body is built up from these cells. This is by no means the case. In every case, however large it is—and even when cell-nuclei travel into it during the cleavage of the border—the nutritive yolk remains a dead accumulation of food, which is taken into the gut during

the amphieme, the small ovum completely divides into cells on segmentation, this is no longer so in the great majority of the vertebrates (cf. *Teleostei*). In these the contractility of the active protoplasm no longer suffices to break up the huge mass of the parent deutoplasm completely into cells; this is only possible in the upper or dorsal part, but not in the lower or ventral section. Hence we find in the primitive fishes a blastula with a small eccentric segmentation-cavity (Fig. 53, *b*), the wall of which varies greatly in composition. The circular border of the gerarial disk which connects the roof and floor of the segmentation-cavity corresponds to the hædomeum at the equator of the segmentation-cavity. At the middle of its border border lies from the beginning of the invagination of the primitive gut

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(Fig. 56 *inf.*) ; it extends gradually from this spot (which corresponds to the Koenenian axis of the amphibia) forward and around, so that the primitive streak becomes first crescent-shaped and then



FIG. 56.—Diagram, *externa (superior)*, of a bird's egg. 1. yolk. 2. yolk-membrane. 3. allantois. 4. chorion. 5. shell membrane. 6. yolk. 7. yolk-membrane. 8. chorion. 9. allantois. 10. shell membrane. 11. shell. (After the Koenenian series.)

circular, and, as it opens wider, surrounds the half of the larger yolk-sac.

Essentially different from the wide-

streak is the narrow-mouthed discoid *stomodeum (or pharynx)* of the *amphibians*, the reptiles, birds, and mammals—between the two—as an intermediate stage—we have the *amphibians* of the *reptiles*. The latter has developed from the *amphibians* of the *gnathostomes* and *diaphons*, whereas the discoid *stomodeum* *gnathos* has been evolved from the *amphibian* *gnathos* by the addition of food-yolk. This change of gastrulation is still found in the remarkable *gnathos* (*Gymnophiona*, *Caudata*, or *Pezzoidea*), serpent-like amphibia that live in moist soil in the tropics, and in many respects represent the transition from the gill-breathing amphibia to the lung-breathing reptiles. Their embryonic development has been explained by the fine studies of the brothers *Sarsen* of *Jaffna* (1907), and those of August *Bauer* of the

The bird's egg is particularly important for our purpose, because most of the chief studies of the development of the vertebrates are based on observations of  
—Jen's egg, during  
—sch. n.

obtain and study, and for this practical and obvious reason very rarely thoroughly investigated. But we can get hens' eggs in any quantity at any time, and, by means of artificial incubation, follow the development of the embryo step by step. The bird's egg differs considerably from the tiny mammal ovum in size, a large quantity of food-yolk accumulating within the original yolk or the protoplasm of the ovum. This is the yellow ball which we commonly call the *yolk* of the egg. In order to understand the bird's egg aright—for it is very often quite wrongly explained—we

and follow it from the very beginning of its development in the bird's ovary. We then see that the original *ovum* is a quite small, naked, and simple cell with a nucleus, not differing in either size or shape from the original ovum of the mammals and other animals (cf. Fig. 13.2). As in the case

of the original or primitive ovum (*protozon*) it is covered with a continuous layer of cells. This is the *chorion*, the *follicle*, from which the ovum afterwards issues. Immediately underneath it the structureless yolk-membrane is secreted in the yolk.

The small primitive ovum of the bird begins very early to take up into itself a quantity of food-stuff through the yolk-membrane, and work it up into the "yellow yolk." In this way the ovum

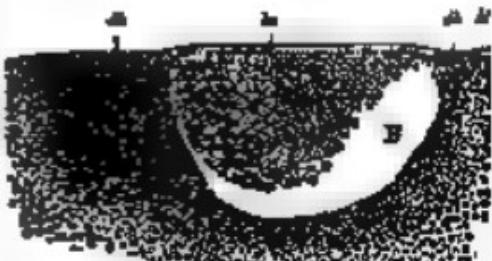
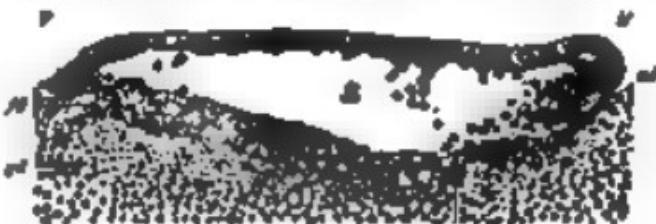


FIG. 57.—Longitudinal section through the blastoderm of

historical and comparative study of these that we can understand the difficult and obscure gastrulation of the annelids.

comes on its second stage (the morula), which is many times larger than the first, but still only a single enlarged cell. Through the accretion of the store of yellow yolk within the ball of protoplasm the nucleus it contains (the germinal vesicle) is forced to the surface of the ball. Here it is surrounded by a small quantity of protoplasm, and with this forms the lens-shaped formative yolk (Fig. 21 A). This is seen on the yellow yolk-ball, at a certain point of the surface, as a small round white spot—the "crown" (germinal disk). From this point a chromatic column of white suspensive yolk (*A*), which contains no yellow yolk-nucleus, and is softer than the yellow form-yolk, proceeds to the middle of the yellow yolk-ball, and forms there a small central globule of white yolk (Fig. 21 A). The whole of this white yolk is not sharply separated from the yellow yolk, which

(Fig. 21) First two spiral segmentations-cells (*A*) are formed from the ovum. These divide into four (*B*), then into eight, sixteen (*C*), thirty-two, sixty-four, and so on. The cleavage of the cells is always preceded by a division of their nuclei. The cleavage-surface between the segmentation-cells appears at the free surface of the trend as folds. The first two divisions are vertical to each other, in the form of a cross (*E*). Then there are two more divisions, which cut the former at an angle of thirty-five degrees. The trend, which thus becomes the germinal disk, now has the appearance of an eight-rayed star. A circular cleavage next taking place round the middle, the eight triangular cells divide into sixteen, of which eight are in the middle and eight distributed around (*C*). Afterwards circular clefts and radial clefts, directed towards the centre, alternate more or less



The 1/2-in.-diameter section of the yolk of a chick (fractured on the left) of the bird (Pheasant) shows the polar body and the germinal disk of the yolk in position, & the yolk-cells, & the germinal disk of the yolk.

shows a slight trace of concretion layers in the hard-shelled egg (Fig. 25 A). We also find in the hen's egg, when we break the shell and take out the yolk, a round small white disk at its surface which corresponds to the trend. But this small white "germinal disk" is now further developed, and is really the germinatrix of the chick. The body of the chick is formed from it alone. The whole white and yellow yolk—*per se*—is without any significance for the formation of the embryo, it being merely used as food by the developing chick. The clear, granular mass of albumen that surrounds the yellow yolk of the bird's egg, and also the hard, chalky shell, are only formed within the evanescent round the impregnated ovum.

When the fertilisation of the bird's ovum has taken place within the mother's body, we find in the lens-shaped stem-cell the progress of the double segmentation

irregularly (*D*, *E*). In most of the avianites the formation of concentric and radial clefts — begins from the very first ; and so also in the hen's egg. But the final outcome of the cleavage-process is once more the formation of a large number of small cells of a similar nature. As in the case of the fish-ovum, these segmentation-cells form a round, interlocked disk, which corresponds to the nucleus, and is embedded in a small depression of the white yolk. Between the lens-shaped disk of the morula-cells and the underlying white yolk a small cavity is now formed by the accretion of fluid, as in the fishes. Thus we get the peculiar and not easily recognizable bladders of the bird (Fig. 21). The small segmentation-cavity (*A*) is very flat and much compressed. The upper or dorsal end (*D*) is formed of a single layer of clear, distinctly separated cells ; this

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corresponds to the upper or animal hemisphere of the triton-blastula (Fig. 45*a*). The lower or ventral wall of the line dividing space (*nav*) is made up of larger and darker segmentation-cells; it corresponds to the lower or vegetal hemisphaera of the blastula of the water-salamander (Fig. 45*ab*). The nuclei of the yolk-cells, which are in this case especially numerous at the edge of the lens-shaped blastula, travel into the white yolk, increase by cleavage, and contribute even to the further growth of the germinative disk by furnishing it with food-stuff.

The Invagination or the folding inwards of the bird-blastula takes place in the

which was described for a long time as the "primitive groove." If we make a vertical section through this part, we see that a flat and broad cleft stretches under the germinal disk forwards from the primitive mouth; this is the primitive gut (Fig. 46*mf*). Its roof or dorsal wall is formed by the folded upper part of the blastula, and its floor or ventral wall by the white yolk (*ovf*), on which a cluster of yolk-nuclei (*ynf*) are distributed. There is a brisk multiplication of them at the edge of the germinal disk, especially in the neighbourhood of the sickle-shaped primitive mouth.

We learn from sections through later stages of this diected bird-gastrula that

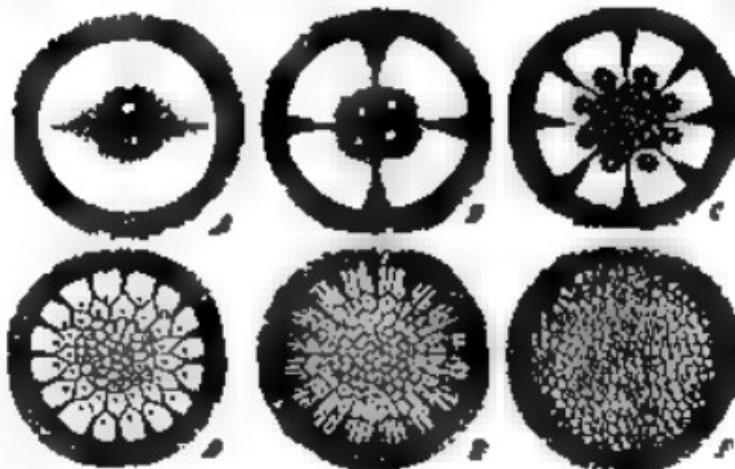


FIG. 46.—Diagrams of diected gastrulation in the bird's egg, magnified about ten times. Only the primitive yolk (*ovf*) is shown to show the division of the germinal disk into the inner, more compact, and larger layer (*gdf*), which does not share in the cleavage, & left out and easily observed by the dark ring (*gr*).

also also at the hinder pole of the subsequent chief axis, in the middle of the hind border of the round germinal disk (Fig. 49*a*). At this spot we have the most brisk cleavage of the cells, hence the cells are more numerous and smaller here than in the fore-half of the germinative disk. The border-swelling or thick edge of the disk is less clear but whiter behind, and is more sharply separated from contiguous parts. In the middle of its hind border there is a white, crescent-shaped groove—Keller's sickle-groove (Fig. 49*a*); a small projecting process in the center of it is called the pickle-lump (*plf*). This important cleft is the primitive mouth,

the primitive gut-wall, extending forward from the primitive mouth as a flat pouch, undermining the whole region of the round flat lens-shaped blastula (Fig. 46*mf*). At the same time, the segmentation-cavity gradually disappears altogether, the folded inner germinal layer (*glf*) raising itself from underneath on the overlying outer germinal layer (*glk*). The typical process of Invagination, though greatly disguised, can thus be clearly seen in this case, as Goette and Ringer, and more recently Duval (Fig. 46), have shown.

The older embryologists (Pander, Baer, Kausk), and, in recent times especially,

## THE GASTRULATION OF THE VERTEBRATE

Hin, KdRitter, and others, said that the two primary germinal layers of the bird's ovum—the oldest and most fragment subject of observation—arose by longitudinal cleavage of a simple germinal disk. In opposition to this accepted view,<sup>1</sup> I affirmed in my *Gastrula Theory* (1873)

its surface. I endeavored to establish this view by the derivation of the vertebrates from one source, and especially by proving that the birds descend from the reptiles, and these from the amphibia. If this is correct, the discoid gastrula of the amniotes must have been formed by



Fig. 4a.



Fig. 4b.

Fig. 4a.—Vertical section of the blastoderm of a hen (*domesticus*). *M*, mesoderm; *v*, viscerum; *m*, mesothelium; *s*, the surface wall facing directly into the air space (visceral cavity) (From Goettl.)

Fig. 4b.—The opercular disk of the hen, which is the beginning of gastrulation. *M*, before invagination; *v*, at the first stage of invagination. (From Goettl.) *M*, mesoderm; *v*, the fore part of the head border; *m*, mesothelium; *s*, surface; *a*, middle layer.

Fig. 4c.—Longitudinal section of the opercular disk of a chick (*domesticus*). *M*, mesoderm; *v*, viscerum; *m*, mesothelium; *s*, the fore and hind part of the surface membrane (or ectoderm); *a*, outer germinal layer; *yellowish*, *yellowish*, and *white*.



Fig. 4c.—Longitudinal section of the opercular disk of the chick (*domesticus*). (From Goettl.) *M*, mesoderm; *v*, viscerum; *m*, mesothelium; *s*, the surface membrane; *a*, outer germinal layer; *yellowish*, *yellowish*, and *white*.

that the discoid bird-gastrula, like that of all other vertebrates, is formed by folding (or invagination), and that this typical process is merely altered in a peculiar way and disguised by the incessant accumulation of food-yolk and the flat spreading of the discoid blastoderm at one part of

the folding-in of a hollow blastoderm, as has been shown by Romer and Resconi of the discoid gastrula of the amphibia, their direct ancestors. The accurate and extremely careful observations of the authors I have mentioned (Goettl, Rauber, and Dörr) have decisively proved this

recently for the birds; and the same has been done for the reptiles by the fine studies of Kupffer, Bonatz, Westholzsch, and others. In the shield-shaped epibranchial disk of the lizard (Fig. 6a), the crocodile, the tortoise, and other reptiles, we find in the middle of the hind border (at the same spot as the sickle groove in the bird) a transverse furrow ( $\gamma$ ), which leads into a flat, pouch-like, blind sac, the primitive gut. The fore (dorsal) and hind (ventral) lips of the transverse furrow correspond exactly to the lips of the primitive mouth (or sickle-groove) in the birds.

The gastrulation of the mammals must

I first advanced this fundamental principle in my essay *On the Gastrulation of Mammals* (1877), and sought to show in this way that I assumed a gradual degeneration of the food-yolk and the yolk-sac on the way from the protogaster —

The ontogenetic process of adaptation," I said, "which has occurred — play of the evolutionary post-nat. of the mammal, is perfectly clear. It is due to the fact that the young of the mammal, whose ancestors were certainly oviparous, now remain a long time in the womb. As the great store of food-yolk, which the oviparous ancestors gave to the egg, became superfluous in their descendants owing to the long carrying in the womb, and the maternal blood in the wall of the uterus made itself the chief source of nourishment, the now useless yolk-sac was bound to atrophy by embryonic atrophy."

My opinion met with little



FIG. 6a.—Epibranchial disk of the lizard (*Sceloporus variabilis*).  $\gamma$ , transverse mouth;  $\alpha$ , mouth;  $\beta$ , epibranchial disk;  $\delta$ , fore and hind gastrulation areas.

in derived from this special embryonic development of the reptiles and birds. This latest and most advanced class of the vertebrates has, as we shall see afterwards, evolved at a comparatively recent date from an older group of reptiles, and all these animals must have come originally from a common stem-form. Hence the distinctive embryonic process of the mammal must have arisen by convergent modifications from the older, — *gast* — of the reptiles and birds. Until I admit this thesis we cannot understand the formation of the germinal layers in the mammals, and thence-

subsequently attacked by Kolle, Hensen, and his followers. However, it has been gradually accepted, and has recently been firmly established by a large number of excellent studies of mammal gastrulation, especially by Robert von Bonatz's studies of the rabbit and bat, Schenck's on the marsupials and rodents, Hooge's and Leberkühn's on the mole, Kupffer and Kolle's on the rodent, Bonatz's on the ruminants, etc. From the general comparative point of view, Carl Rabl in his theory of the mammals, Oscar Hertwig in the latest edition of his *Handbuch* (1892), and Hubrecht in his *Studies in Mammalian Embryology* (1894), have supported the opinion, and sought to derive the peculiarly modified gastrulation of the mammal from that of the reptile.

In the meantime (1884) the studies of Wilhelm Beesley and Caldwell provided a proof of the long-suspected and interesting fact, that the lowest mammals, the monotremes, lay eggs, like the birds and reptiles, and are not viviparous like the other mammals. Although the gastrulation of the monotremes was not really known until studied by Richard

Section in 1894, there could be little doubt, in view of the great size of their food-yolk, that their extra-embryonic was discoid, and led to the formation of a wide-mouthed monotreme, as in the

higher mammals. In these the gastrulation proceeds in two phases, as Semon rightly observes : firstly, formation of the ectoderm by cleavage at the centre and further growth at the edge ; secondly, invagination. In the monotremes more primitive conditions have been retained latter than in the reptiles and birds. In the latter, before the commencement of the gastrula-folding, we have, at least at the pachynony, a two-layered embryo facing keen the cleavage. But in the monotremes the formation of the ectodermic ectoderm does not precede the invagination, hence in this case the construction of the germinal layers is less modified than in the other amniotes.

The marsupials, a second sub-class, stand next to the oviparous monotremes, the oldest of the mammals. But as in this case the food-yolk is already yolked, and the little ovum develops within the mother's body, the partial cleavage has been reconverted into total. One section of the marsupials will show points of agreement with the monotremes, while another section of them, according to the splendid investigations of Solander, form a connecting-link between these and the placentals.

The fertilized ovary of the opossum (*Didelphis*) divides, according to Solander, into two, then four, then eight equal parts; hence the segmentation is at first

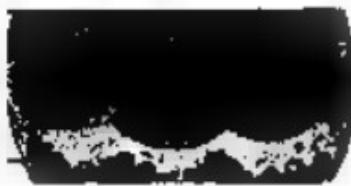


Fig. 4.—Opossum (*Didelphis*). A longitudinal section of the first division of the yolk, & a yolkless membrane.

one of the reptiles and birds. Hence I had, in 1876 (in my study on *The Osteology and Ova—segmentation of Amniotes*), counted the monotremes among the discoblastic vertebrates. This hypothesis

afterwards, by the careful observations of Huxley, he gave in the second volume of his great work, *Zoological Journal of Atavismus* (1884), the first description and correct explanation of the discoid gastrulation of the monotremes. The ferried eggs of the two living monotremes (*Echidna* and *Tachyglossus*) are balls of ovo-fibra of an inch in diameter, enclosed in a stiff shell; but they grow considerably during development, so that when laid the egg is three times as large. The structure of the plentiful yolk, and especially the relation of the yellow and the white yolk, are just the same as in the reptiles and birds. As with these, partial cleavage takes place at a spot on the surface at which the small forebrain cells and the nucleus it occupies are found. First is formed a lens-shaped circular germinal disk. This is made up of several strata of cells, but it spreads over the yolk-ball, and thus becomes a one-layered blastula. If we then imagine the yolk to continue to be dissolved and replaced by a clear fluid, we have the characteristic blastula of the



Fig. 5.—Opossum (*Didelphis*). A second part of the blastula, a yolkless part, an endoderm-cell of the midbrain, an intermediate cell, a yolk-granule, & a yolkless membrane.

larva homogenous. But in the case of the cleavage a larger cell, distinguished by its less clear plasma and its containing more yolk-granules (the mother cell of the ectoderm, Fig. 64, 12),

separates from the others; the latter multiply more rapidly than the former. As, further, a quantity of fluid gathers in the morula, we get a round blastula, the wall of which is of varying thickness, like that of the amphioxus (Fig. 55 A) and the amphibia (Fig. 44). The upper or animal hemisphere is formed of a large number of small cells; the lower or vegetal hemisphere of a small number of large cells. One of the latter, the magnified by its size ( $P'$ )—as, lies at the vegetal pole of the blastula, at the point where the primitive streak afterwards appears—in is the mother-cell of the endoderm. It now begins to multiply by cleavage, and the daughter-cells (Fig. 45 C) spread out from this spot

gastroderm (Fig. 56) gradually changes into globular, a larger quantity of fluid accumulating in the vesicle. At the same time, the ectoderm spreads further and further over the inner surface of the endoderm ( $\beta$ ). A globular formed, the wall of which of two thin simple strata of cells: cells of the outer germlinal layer rounder, and those of the inner layer flatter. In the region of the primitive streak ( $\beta$ ) the cells are less flattened, and markedly wrinkly. From this point—*from the head (ventral) lip of the primitive streak*, which extends in a central cleft, the primitive groove—the gastrulation of the remainder proceeds.

Gastrulation is still more modified and

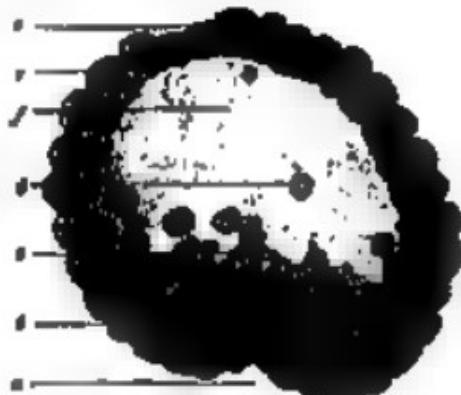


FIG. 45.



FIG. 46.

FIG. 45.—STAGES OF THE GASTRULATION IN THE EMBRYO OF RANA DORSALIS 30 HOURS OLD.  $y$ , yolk;  $gr$ , germ ring;  $bl$ , blastoderm;  $bc$ , blastocoel.  $P'$ , a primitive streak at the vegetal pole.  $\beta$ , representative points of various germlinal layers of the rounded body with distinct card (epiblast) and yolk (hypoblast).

FIG. 46.—EARLY STAGES OF THE GASTRULATION IN DENDROBLASTUS (about eight hours old).  $y$ , yolk;  $gr$ , germ ring;  $bl$ , blastoderm.

over the inner surface of the blastula, though at first only over the vegetal hemisphere. The less clear ectodermic cells ( $\beta$ ) are distinguished at first by their rounder shape and darker color from the higher, clearer, and larger endodermic cells ( $\alpha$ ); afterwards both are greatly flattened, the inner endodermic cells more than the outer.

The unucleated yolk-balls and ova (Fig. 65 d) that we find in the field of the blastula in these starfishes are very remarkable; they are the relics of the atrophied food-yolk, which was developed in their ancestors, the conchostraceans, and in the reptiles.

In the further course of the gastrulation of the opossum the oval shape of the

embryo congegeterically in the placentals than in the marsupials. It was first accurately known to us by the distinguished investigations of Edward Van Beneden in 1875, the first object of study being the ovum of the rabbit. But as soon also belongs to this sub-class, and as has as yet unstudied gastrulation cannot be essentially different from that of the other placentals, it merits the closest attention. We have, in the first place, the peculiar feature that the two first segmentation-cells that proceed from the cleavage of the fertilized ovum (Fig. 66) are of different sizes and natures; the difference is sometimes greater, sometimes less (Fig. 66). One of these first daughter-cells of the ovum is a little

larger, clearer, and more transparent than the other. Further, the smaller cell takes a colour in carmine, iodine, etc., more strongly than the larger. By repeated cleavage of  $\alpha$  is a macula formed, and from this a blastula, which changes in a very characteristic way into the greatly rounded gastrula. When the number of the segmentation-cells

is (in the rabbit) about twenty hours after impregnation the future embryo forms very like the archigastria (Fig. 72). The spherical embryo consists of a central mass of thirty-two soft, round cells with dark nuclei, which are flattened into polygonal shapes by mutual pressure, and colour dark-brown with osmotic acid (Fig. 72 d). This dark central group of cells is surrounded by a lighter spherical membrane, consisting of star-shaped, small, and irregularly arranged cells which lie close together in a single stratum, and only colour slightly in osmotic acid (Fig. 72 e). The authors who regard this embryo as the primary gastrula of the placental coöccide the outer layer as the ectoderm and the inner as the endoderm. The amniotic membrane is only interrupted at one spot, one, two, or three of the ectodermic cells being loose there. These form the olfactopore, and fill up the mouth of the gastrula (e). The central primitive gastrula (d) is full of endodermic cells. The unusual type of the mammalian gastrula is accentuated at this stage. However, opinions still differ considerably as to the real nature of this "pre-gastrula" of the placental and its relation to the blastula into which it is converted.

As the gastrulation proceeds a large spherical blastula is formed from the peculiar solid amphioxostyle of the placental, as we now see in the case of the mammal. The accumulation of fluid in the solid gastrula (Fig. 73 f) leads to the formation of an ectocytic cavity, the group of the darker entodermic cells ( $\beta\gamma$ ) remaining directly attached at one spot with the round enveloping stratum of the lighter ectodermic cells ( $\alpha\delta$ ). This spot corresponds to the original primitive mouth (prostoma or blastostome). From this important spot the inner gastrula layer spreads all round on the inner surface of the outer layer, the cell-strata of which forms the wall of the hollow sphere; the astension proceeds from the vegetal towards the animal pole.

The oogenetic gastrulation of the placental has been greatly modified by secondary adaptations in the various groups of the most advanced and youngest sub-class of the mammals. Thus, for instance, we find in many of the rodents (guinea-pig, mice, etc.) apparently a temporary invagination of the two gastrula layers. This is due to a thin, "indarval wall" by what is called the "girdle," a plug-shaped growth of Rucker's "roof-layer." It is a thin layer of flat epithelial cells, that is freed from the surface of the blastula in some of the rodents; it has no more significance in connection with the general course of placental gastrulation than the amniotic does in connection with the

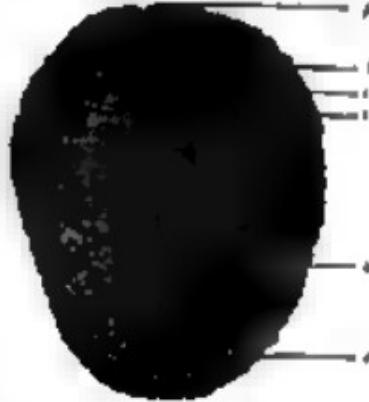


FIG. 72.—Gastrulation process through the early stages of development (Fig. 72). (From Wiedemann's *Praktische Entwicklungsgeschichte der Wirbeltiere*.)

globular shape in the blastula of some of the ungulates. In some pigs and ruminants it grows into a thread-like, long and thin tube.

Thus the gastrulation of the placental, the primitive form, is reduced to the original type, the invagination of the undifferentiated blastula. It is seen that the foliose part of the blastoderm does not form a completely closed (only open at the primitive mouth) blind sac, as is usual; but this blind sac has a wide opening at the ventral curve (opposite to the dorsal mouth); and through this opening the primitive gut communicates from the first with the embryonic cavity of the blastula. The folded crest-shaped

## THE GASTRULATION OF THE VERTEBRATE

ectoderm grows with a fine circular border on the inner surface of the endoderm towards the vegetal pole; when it has reached this, and the inner surface of the blastula is completely covered over, the primitive gut is closed. This remarkable

process (the reptiles), is arrested. This proves the essential unity of gastrulation in all the vertebrates, in spite of the striking differences in the various classes.

In order to complete our consideration of the important processes of segmenta-

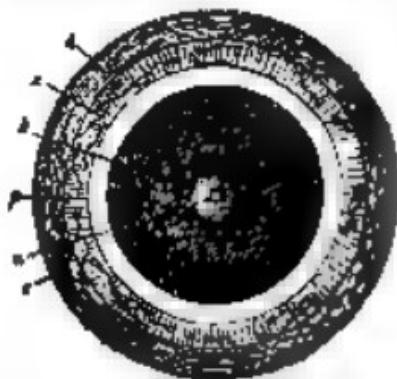


FIG. 25.—Egg-cell of the coelenterate *Ciona intestinalis*. A longitudinal section showing the development of the mesoblast, a median yolk-sac, and a large yolk-cell.

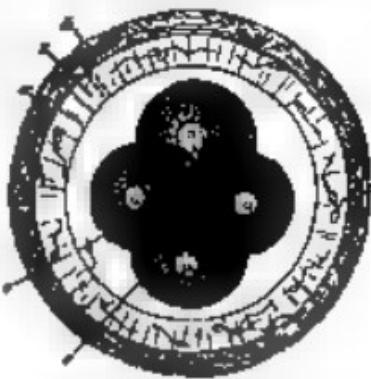


FIG. 26.—The first four segmentation-spots of *Ciona intestinalis* (C. intestinalis, the red starfish). (After Hertwig.)



FIG. 27.—Indirect cleavage of the egg-cell from the rabbit. The egg-cell has divided into two unequal parts, one higher (a) and one lower (b), a new yolk-sac, a outer yolk-sac membrane, a dead yolk-cell.



FIG. 28.—Segmented ovule with eight eggs (pig). The egg-cell (from the rabbit), a four-layered yolk-sac, a new yolk-sac, a outer yolk-sac membrane, a dead yolk-cell.

direct transition of the primitive gut-cavity into the segmentative-cavity as explained simply by the assumption that in most of the mammals the yolk-sac, which is still possessed by the older forms of the class (the monotremes) and

fish and gastrulation, we will, in conclusion, cast a brief glance at the fourth chief type—superficial segmentation. In the vertebrates this form is not found at all. But it plays the chief part in the large class of the arthropods—the insects,

## THE GASTRULATION OF THE VERTEBRATE

spiders, myriapods, and crabs. The distinctive form of gastrula that comes of it is the "vesicular gastrula" (*perivitelline*).

In the ova which undergo this superficial cleavage the formative yolk is sharply divided from the nutritive yolk, and in the preceding cases of the sort of birds, reptiles, fishes, etc.; the formative yolk alone undergoes cleavage. But while in the ova with direct gastrulation the formative yolk is not at the center, but at one pole of the unicellular mass, and the food-yolk gathered at the other pole, in the ova with superficial cleavage we find the formative cells spread over the whole surface of the ovum, it encloses spherically the food-yolk, which is accumulated in the middle of the egg. Segmentation only affects the former, not the latter, it is bound to be

seen by it.

As a rule, it proceeds in regular geometrical progression. In the end the whole of the formative yolk divides into a number of small and homogeneous cells, which lie close together in a single stratum on the entire surface of the ovum and form a superficial blastoderm. This blastoderm is a simple, completely closed vesicle, the internal cavity of which is entirely full of food-yolk. This real blastula only differs from that of the primitive ova in its chemical composition. In the latter the content is a clear or a watery jelly;

beginning, there is no difference between the membranes.

The two stages reader

When the blastula is fully formed, viz., the last stage of the first division, the important folding or invagination that determines gastrulation. The space between the inner-layer and the gut-layer (the remainder of the segmentation-cavity) remains full of food-yolk, which is gradually used up. This is the only material difference between our vesicular gastrula (*perivitelline*) and the original form of the bell-gastrula (*antiperitrophic*). Clearly the one has been developed from the other in the course of time, owing to the accumulation of food-yolk in the center of the ovum.<sup>1</sup>

We must count it an important advance but we are then in a position to reduce

"... embryonic phenomena in the different groups of animals to three principal forms of segmentation and gastrulation. Of these four forms we must regard one only as the original palingenetic, and the other three as teleogenetic and derivative. The unipolar, the bipolar, and the superficial segmentation have all clearly arisen by secondary adaptation from the primary segmentation, and the chief cause of their development has been the gradual formation of the food-yolk, and the increasing distance between animal and vegetal halves of the ovum, or between ectoderm (skin-layer) and endoderm (gut-layer)."

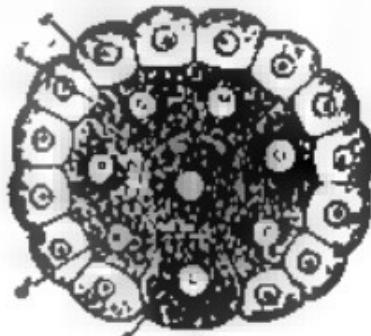


Fig. 10.—Diagram of the vesicular gastrula of the frog. A longitudinal section through the egg, a cross-section thirty-four hours old, showing the outer nutritive layer and the inner layer containing the yolk. The yolk is filled with a granular substance, and occupying the center of the yolk is a small cavity (yolk-sac) in the shape of a funnel-shaped vesicle (yolk-sac).

The numbers of careful studies of animal gastrulation that have been made since have completely established the

In I first advanced in the years 1870-76. For a time they were greatly disputed by many embryologists. Some said that the original embryonic form of the mesozoan was not the gastrula, but the "phota,"—a double-walled vesicle with closed cavity and without mouth-aperture; the latter was supposed to pierce through gradually. It was afterwards shown that this phota (found in several sponges, etc.) was a later evolution from the gastrula.

<sup>1</sup> On the relation of all forms of gastrulation to the original palingenetic form see especially the last section of Haeckel's *Die Entwicklungsgeschichte der Thiere* (1874), Part I.

It was also shown that what is called determination—the rise of the two primary germinal layers by the folding of the surface of the blastoderm (for instance, in the Cyclopidea and other insects)—was a secondary formation, due to heterogenetic

processes. The primary germinal layers, which attach themselves to the inner wall of the blastoderm, and form a second intern—epiblastic layer—that is to say, the entoderm. In these and many other contributions of modern embryology the first requisite for clear and natural explanation

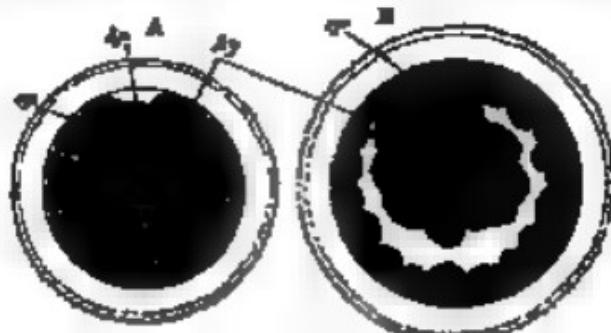


FIG. 53.—Gastrula of the rabbit. A, a solid spherical cluster of cells, B, showing how the embryo begins to form mouth, &c., outside of B.

variations from the original invagination of the blastula. The same may be said of what is called "immigration," to which certain cells or groups of cells are detached from the simple layer of the blastoderm, and transmigrate the interior of the blastula.

is a careful and discriminative distinction between palingenetic (hereditary) and conogenous (adaptive) processes. If this is properly attended to, we find evidence everywhere of the biogenetic law.

## CHAPTER X. THE CELOM THEORY

The two "primary germinal layers" which the gastral theory has shown to be the first foundation in the construction of the body are found in the simplest forms throughout life only in animals of the lowest grade—in the gastrulae, ovaules (the stem-form of the sponges), hydra, tritellaria, and simple animals. In all the other animals now known—formed subsequently between these two primary body-layers, and these are generally comprehended under the title of the middle layer, or mesoderm. As a rule, the

various products of this middle layer afterwards constitute the great bulk of the animal frame, while the original entoderm, or internal germinal layer, is restricted to the lining of the alimentary canal and its glandular appendages; and, on the other hand, the ectoderm, or external germinal layer, furnishes the outer covering of the body, the skin and nervous system.

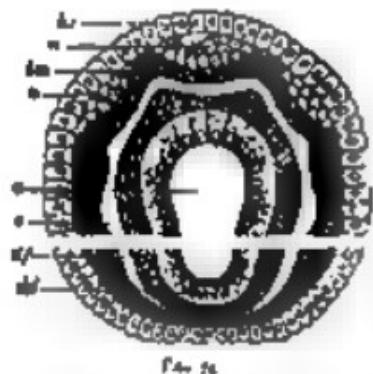
so large groups of the lower such as the sponges, corals, and in, the middle germinal layer

is a single connected mass, and of the body is developed from it; these have been called the three-layered animals. In opposite layered animals described. Like the two animals, they have no body-cavity—that is to say, no cavity distinct from the alimentary system. On the other hand,

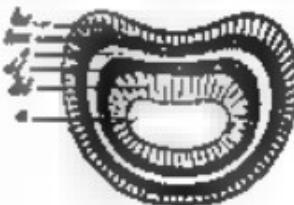
develop from the two primary layers. To the same class belong all true vertebrates (excepting the placoderm), and also those evolved from them - molluscs, annelids, arthropods, tunicates, and vertebrates.

metameric . . . mal-  
body, is the oldest and most important  
organ of all the metamer, and, together  
with the primitive mouth, is formed in  
the first week of life. In the amniote  
embryo, it is only at a much later stage that  
the body-cavity, which is entirely wanting  
in the caeciliae, is developed "u  
of the metamer between 1

the body wall. The two cavities are entirely different in content and purpose. The alimentary cavity (*esophagus*) serves the purpose of digestion; it contains water and food taken from without, as well as the pulp (*chymus*) formed from



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Fig. 29 and 30.—Diagram of the four secondary  
anastomoses, the last two through the  
liver, which are shown in black. Fig. 31  
is a diagram of a portion of the ventral  
system of venous drainage, and anastomoses. It  
demonstrates a crossing of the tributaries  
between a portion of the hepatic

The high-cervitis (*caruncula*) is therefore a new acquisition of the animal body, much younger than the olfactory system, and of great importance. I first pointed out this fundamental significance of the caruncula in my *Aborigines as the Springer* (1872), in the section which draws a distinction between the body-cavity and the gut-cavity, and which follows immediately on the germ-layer theory and the ancestral tree of the animal kingdom (the first branch of the gastraea theory). Up to that time these two principal cavities of the animal body had been confused, or very imperfectly distinguished; chiefly because Leuckart, the founder of the *caruncularia* group (1848), has attributed a body-cavity, but not a gut-cavity, to these lowest metazoa. In reality, the truth is just the other way about.

self and its glandular appendages, and also contain the actual products and a certain amount of blood or lymph, in fluid that is circulated through the veins.

As soon as the body-cavity appears, the ventral wall is found to be separated from the overlying body-wall, but the two continue to be directly connected at certain points. We can also then always distinguish a number of different layers of tissue in both walls—at least two in each. These three-layers are formed originally from four different simple cell-layers, which are the much-dispersed four secondary germinal layers. The outermost of these, the skin-mucous-layer (FIGS. 74, 75 A), and the innermost, the gut-gland-layer (*id.*), remain at first simple epithelia or covering-layers. The skin covers the outer

## THE OOCYCLE THEORY

surface of the ventral wall; hence they are called confining or limiting layers. Between them are the two middle-layers, *soblaeia*, which enclose the body-cavity.



Fig. 22.—Diagram of embryo showing the four secondary germinal layers.

— permanent name.

The four secondary germinal layers are so distributed in the structure of the body in all the coelomaria (or all metazoa that have a body-cavity) that the outer two, joined flat together, constitute the body-wall, and the inner two the ventral walls are separated by the stom. Each of the walls is a limiting layer.

tissues, and glands, and nerves, middle layers form the great bulk of the fibrous tissue, muscle, and connective matter. Hence the latter have been called fibrous or muscular layers. The outer middle layer, which lies on the outer side of the skin-muscle-layer, is the skin fibre-layer, the inner middle layer, which attaches from without to the ventral glandular layer, is the ventral fibre-layer. The former is usually called briefly the peritoneal, and the latter the visceral layer or mesoderm. Of the many different names that have been given to the four secondary germinal layers, the following are:

1. Skin-muscle-layer (outer limiting-layer)	2. Fibrous-layer (outer middle-layer)	3. Peritoneal-layer (inner middle-layer)	4. Ventral-glandular-layer (innermost).
The two middle-layers			5. Body-cavity.

The first scientist to recognise and clearly distinguish the four secondary germinal layers was Baer. It is true he was not quite clear as to their origin and further

several mistakes in detail in explaining them. But, on the whole, their great importance did not escape him. However, as later years his view had to be given up in consequence of more accurate observations. Romak then propounded a three-layer theory, which was generally accepted. This theory of cleavage, however, began to give way thirty years when Kowalevsky (1871) showed in the case of *Sagitta* (a very clear typical subject of gastrulation) the middle germinal layers and the two outer layers arise not by cleavage, but

by folding—by a secondary invagination or folding produced from the primitive mouth, at the two sides of which (right and left) a couple of pouches are formed. As these evolute-pouches or cotyledons detach themselves from the primitive gut, a double body-cavity is formed (Figs. 23-6).

The same kind of coelum-formation in *Sagitta* was afterwards found in *Kowalevskyia* in *Brachiopterus*.

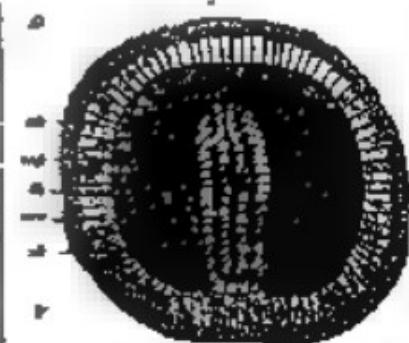


FIG. 23.—Diagram of *Sagitta*, in section. (From Kowalevsky.) A dorsal side; B ventral side; C outer middle-layer, i.e. ventral muscle-layer; D body-cavity; E inner middle-layer; F innermost layer, i.e. inner germinal layer.

In 1859—E. Ray Lankester and F. Balfour. On the strength of these and other studies, as well as much extensive research of their own, the brothers Oscar and Michael Hertwig constructed in 1881

the Cecloem Theory. In order to appreciate fully the great merit of this illuminating and helpful theory, one must remember what a class of contradictory views was then represented by the "problem of the Cecloem," or the much-disputed "question of the origin of the middle germinal layer." The cecloem theory brought these right and left into this mutual confusion by establishing the following points: 1. The body-cavity originates in the great majority of animals (especially in all the vertebrates) in the same way as in insects—a couple of pouches or sacs are formed by folding inward at the primitive mouth, between the two primary germinal layers; as these pouches detach from the primitive gut, a pair of coelom-sacs (right and left) are formed, the cavities of these products being body-cavity. 2.

coelomocytes develop not as a pair of hollow pouches, but as solid layers of cells (in the shape of a pair of intersegmental streaks)—as happens in the higher vertebrates—we have a secondary body-covering modification of the primary (epiblastic) structure, the two walls of the pouches, inner and outer, have been pressed together by the expansion of the large yolk. 3. Hence the second

from the first of two genetically distinct layers, which do not originate by the division of a primary simple middle layer (as Meekins supposed). These two middle layers have, in all vertebrates, and the great majority of the invertebrates, the same radical significance for the construction of the animal body: the inner middle layer, or the visceral mesoderm (Gut-fibre-layer), attaches itself to the original entoderm, and forms the fibro-muscular, and connective part of the muscular wall; the outer middle layer, or the parietal mesoderm (sheath-fibre-layer), attaches itself to the original ectoderm, and forms the fibro-muscular, and connective part of the body-wall. 4. It is only at the point of origination, the primitive mouth and its vicinity, that the two secondary germinal layers are directly connected; from this point the two middle layers advance forward separately between the two primary germinal layers, to which they severally attach themselves. 5. The further separation or differentiation of the four secondary germinal layers and their division into the various tissues and organs take place especially in the later form-part or head of the embryo, and

which becomes from there towards the primitive mouth.

All regions in which the body-cavity discontinuity occurs as this way from the primitive gut (vertebrates, cephalopods, echinoderms, articulates, and a part of the molluscs) were comprised by the Hertwigs under the title of entomesa, and were contrasted with the other groups of the pseudocoel (with false body-cavity) and the coelostomes (with no body-cavity). However, the radical distinction and the rules as to classification which it occasioned have been shown to be untenable. Further, the objective difference in transformation which the Hertwigs set up between the entomesa and pseudocoel cannot be measured!

For these and other reasons their paleo-theory has been much criticized and partly



FIG. 5.—Schem. of a young embryo. (From Hertwigs.) 1. cerebral cortex; 2. eye; 3. heart; 4. liver; 5. lungs; 6. kidneys; 7. bladder; 8. rectum; 9. recto-uterine duct; 10. recto-uterine duct.

abandoned. Nevertheless, it has rendered a great and lasting service in the solution of the difficult problem of the mesoderm, and a central part of it will certainly be retained. I consider it an essential mark of the theory that it has established the identity of the development of the two middle layers in all the vertebrates, and has traced them as convergent modifications back to the original palaeozoic forms of development that we still find in the cephalopods. Carl Rabl comes to the same conclusion in his *Theory of the Mesoderm*, and so do Ray-Lankaster, Rausch, Kupffer, Racker, Schultze, Hatachov, and others. There is a general agreement in these and many other recent writers that all the different forms of coelom-formation, like those of gastrulation, follow one and the same strict invagination law in the most vertebrates than; in spite of their apparent differences, they

are all, only cycogenetic modifications of one palingenetic type, and this original type has been preserved for us down to the present day by the invaluable amphioxus.

But before we go into the regular confirmation of the amphioxus, we will glance at that of the arrow-worm (*Sagitta*), a remarkable deep-sea worm that is interesting in many ways for comparative anatomy and ontogeny. On the one hand, the transparency of the body of the embryo, and, on the other hand, the typical simplicity of its embryonic development, make the sagitta a most instructive object in connection with various problems. The class of the Ctenophora, which is only represented by the cognate genera of *Sagitta* and *Synidiotrema*, is, in another respect

afterwards anomalous. The two sacs are at first separated by a couple of folds of the entoderm (Fig. 76 A), and are still connected with the primitive gut by wide apertures; they also communicate for a short time with the dorsal side (Fig. 77 A). Soon, however, the coelom-pouches completely separate from each other and from the primitive gut, at the same time they enlarge so much that they close round the primitive gut (Fig. 78). But in the middle line of the dorsal and ventral sides the pouches remain separated, there approaching walls joining here to form a thin vertical partition, the mesenteric fold (Fig. 79). Thus *Sagitta* has throughout life a double body-cavity (Fig. 78 B), and the gut is situated in the mid-wall folds above and below by a mesenteric—below



FIG. 79.

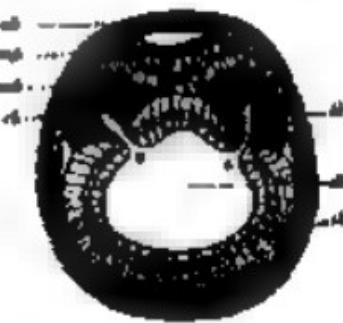


FIG. 78.

FIG. 79 AND FIG. 80.—TRANSVERSE SECTION OF SAGITTA LARVA. (From Moulton.) FIG. 79 IS THE TRANSVERSE SECTION OF COELOM FORMATION (WITH MID-GUT REMOVED). FIG. 80 IS THE SAME, WITH FOUR GERMAL SEGMENTS, AN ANAL POLE, AND MID-GUT REMOVED. IN BOTH PLATES, UP = MEDIAN, DOWN = DORSAL, AND \* INDICATES THE COELOM-POUCHES; A = MID-GUT.

also a most remarkable branch of the establishment-stem. It was therefore very gratifying that Oscar Herring (1909) fully explained the anatomy, classification, and evolution of the Chondrogastridae in his careful monograph.

The spherical blastula that arises from the impregnated ovum of the sagitta is converted by a folding at one pole into a typical arthropodula, entirely similar to that of the *Annelida* which I described (Chapter VIII., Fig. 39). This oval, mesial-cup-larva (circular in section) becomes bilateral (or tri-axial) by the growth of a couple of coelom-pouches from the primitive gut (Figs. 76, 77). To the right and " -shaped fold appears towards the top pole (where the permanent mouth, or,

by the ventral stomodaeum (Fig. 1), and above by the dorsal stomodaeum (Fig. 2). The inner layer of the two coelom-pouches (Fig. 3) attaches itself to the entoderm (Fig. 4), and forms with it the visceral wall. The outer layer (Fig. 5) attaches itself to the ectoderm (Fig. 6), and forms with it the outer body-wall. Thus we have in *Sagitta* a perfectly clear and simple illustration of the palingenetic confirmation of the entocotyle. This paleogenetic fact is the more important, as the greater part of the two body-cavities in *Sagitta* changes afterwards into sexual glands—the female or female part into a pair of ovaries, and the male or male part into a pair of testicles.

Conjugation takes place with equal cleavage and transparency in the case of

the amphioxus, the lowest vertebrates, and its nearest relatives, the invertebrates imprecates, the sea-squirts. However, in these two stems, which we class together as Chordata, this important process is more complex, as two other processes are associated with it—the development of the chorda from the entoderm and the separation

of the medullary plate or nervous centre from the ectoderm. Here again the peculiar amphioxus has preserved to our own time by tenacious heredity the

while it has been lost or less retained by embryonic adaptation in all the other vertebrates (with shells). Hence we must once more thoroughly understand the pulvinigerous embryonic features of the amphioxus before we go on to consider the congeneric forms of the Craniota.

borders of the concave medullary plate fold towards each other and grow underneath the horny-plate, a cylindrical tube is formed, the medullary tube (Fig. 83 a); this quickly detaches itself altogether from the horny-plate. At each side of the medullary tube, between it and the alimentary tube (Figs. 79-83 d), the two parallel longitudinal folds grow out of the dorsal wall of the alimentary tube, and form the two circoli-pouches (Figs. 80 and 81 A). This part of the entoderm,

of the middle germinal layer, is shown darker than the rest of the inner germinal layer in Figs. 79-82. The edges of the folds meet, and thus form closed tubes (Fig. 81 a-macros).

During this interesting process the outline of a third very important organ,

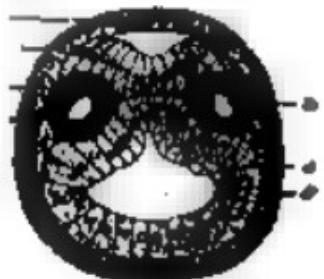


FIG. 81.



FIG. 82.

FIG. 81 and 82.—Transverse sections of amphioxus embryo. FIG. 81 at the stage with the complete ring of the inner germinal layer. A, nervous centre; B, body-cavities; C, middle germinal layer (dark); D, epidermis; E, outer germinal layer; F, ventral surface; G, dorsal surface; H, medullary tube.

The deformation of the amphioxus, which was first observed by Kupferleben in 1867, has been very carefully studied since by Haeselius (1881). According to him, there are first formed on the bilateral gravulae we have already considered (Figs. 36, 37) three parallel longitudinal folds—one single entoderm fold in the central line of the dorsal surface, and a pair of ectodermic folds at the two sides of the former. The broad entoderm fold that first appears in the middle line of the flattened dorsal surface, and forms a shallow longitudinal groove, is the beginning of the central nervous system, the medullary tube. Thus the primary outer germinal layer divides into two parts, the middle medullary plate (Fig. 81 a-p) and the horny-plate (a'), the beginning of the outer skin or epidermis. As the parallel

the chorda or axial rod, is being formed between the two circoli-pouches. This first formation of the skeleton, a solid cylindrical cartilaginous rod, is formed in the middle line of the dorsal primitive gut-wall, from the entodermic cell-trunk that remains bare between the two circoli-pouches (Figs. 79-81 a). The chorda appears at first in the shape of a flat longitudinal fold or a shallow groove (Figs. 80, 82); it does not become a solid cylindrical cord until after separation from the primitive gut (Fig. 82). Hence we might say that the dorsal wall of the primitive gut forms three parallel longitudinal folds at this important period—one single fold and a pair of folds. The single-fold becomes the chorda, and the immediately below the groove of the entoderm, which becomes the medullary

tube; the pair of folds to the right and left lie at the sides between the future and the latter, and form the coelom-pouches. The part of the primitive gut that remains after the cutting off of these three dorsal primitive segments is the post-

(Figs. 83, 84, in the third period of development according to Haeckel). (Sternberg and Plineus give the name of *coelomite* or *coelomite* to young fish larvae.) I ascribe the greatest phylogenetic significance to it, as it is found in all the chorda-



FIG. 83.



FIG. 84.

FIG. 83 and 84.—Diagrams of the coelomites. FIG. 83: Spanish leech-like annelid from the left. FIG. 84: brachio-rotifer. From Haeckel. In FIG. 83 the segment-rings are omitted, in order to show the coelomite more clearly. The first three segments, i.e., forebrain, midbrain, & medulla, are well developed, whereas the remaining 12 segments are represented by small, irregular, & somewhat indistinct structures. FIG. 84 shows the first four segments, i.e., forebrain, midbrain, & medulla, & a slightly enlarged fifth segment, a coelomite. A prominent longitudinal nerve cord runs through the nervous system, which is surrounded by a thin-walled, somewhat irregular, and somewhat irregular layer of the coelomite, consisting of the segmental epidermis.



FIG. 85.



FIG. 86.

FIG. 85 and 86.—Diagrams of the coelomites. FIG. 85: Spanish leech-like annelid from the left; FIG. 86: brachio-rotifer (slightly diagrammatic). Remaining as in FIG. 83 and 84.

ment gut; its entoderm is the gut-gland-layer or ecteric layer.

I give the name of *chordite* or *chordozoa* to the embryonic stage of the vertebrate organism which is represented by the amphioxus larva at this period

(annelides as well as vertebrates) at essentially the same form. Although the metamorphosis of fish-yolk greatly modifies the form of the chordite in the higher vertebrates, it remains the same in its main features throughout. In all

cases the nerve-tube ( $\omega$ ) lies on the dorsal side of the bilateral, worm-like body, the gut-tube ( $Z$ ) on the ventral side, the chorda ( $fob$ ) between the two, on the long axis, and the coelom pouches ( $fe$ ) at each side. In every case there

arose from an ancient coelomic ancestral factor, which we may call Chordia. We should regard this long-extinct Chordia. If it were still in existence, as a special class of unsegmented worm (*chondrus*). It is especially noteworthy that neither

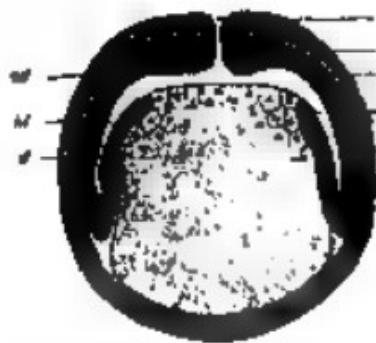


FIG. 8.

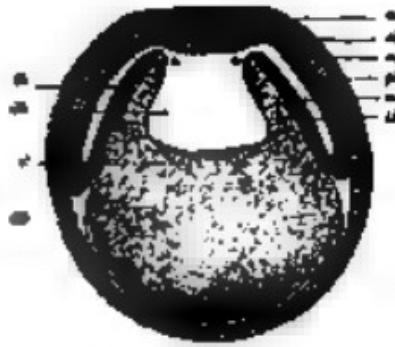


FIG. 9.

FIG. 8 and 9.—Diagrams of the typical section of segmented embryos of vertebrates. (From Haeckel.) FIG. 8 shows regions before the primitive mouth. FIG. 9 shows regions before the primitive mouth, a primitive mouth, and primitive gut.  $\alpha$ , body;  $\beta$ , gut;  $\gamma$ , coelom;  $\delta$ , mesoderm;  $\epsilon$ , endoderm;  $\eta$ , coelomic pouches;  $\zeta$ , chorda;  $\rho$ ,  $\sigma$ ,  $\tau$ , water and non-parenchymal parts;  $\omega$ , nerve-tube;  $\chi$ , nervous system;  $\psi$ , peritoneum;  $\varphi$ , coelom.



FIG. 10.

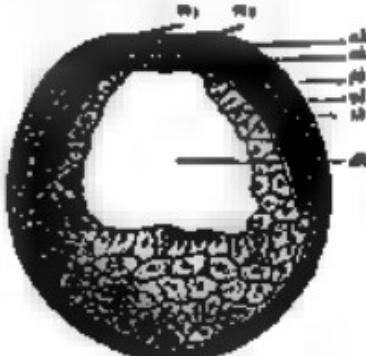


FIG. 11.

FIG. 10 and 11.—Transverse section of unsegmented embryos of fishes. (From Haeckel.) FIG. 10 shows almost the present mouth. FIG. 11 shows in front of the primitive mouth, a primitive mouth, a gut-tube, a coelom,  $\alpha$ , mesoderm,  $\beta$ , water and  $\gamma$ , outer germinal layer;  $\eta$ , coeloid and  $\psi$ , nervous middle layer;  $\omega$ , epidermis;  $\varphi$ , coelom.

primitive organs develop in the same way from the germinal layers, and the same organs always arise from them in the mature chorda-animal. Hence we may conclude, according to the laws of the theory of descent, that all these chordas or chordata (tunicates and vertebrates)

the dorsal nerve-tube nor the ventral gut-tube, nor even the chorda that lies between them, shows any trace of articulation or segmentation; even the two coelomic sacs are not segmented at first although in the epiblast they quickly divide into a series of parts by transverse

folding). These ontogenetic facts are of the greatest importance for the purpose of learning those ancestral forms of the vertebrates which we have to seek in the group of the unarticulated vertebrates. The colom-pouches were originally several glands in these ancient chordates.

From the evolutionary point of view the colom-pouches are, in any case, older than the chorda; since they like the dorsal

in the same way as in the chordons in a number of invertebrates which have no chorda (for instance, Segula, Figs. 26-29). Moreover, in the amphioxus the first nucleus of the chorda appears later than that of the colom-pouches. Hence we must, according to the biogenetic law, deduce a special intermediate form between the gnathostomes and the chordons, which we will call *coelocordate*, an unarticulated, acoelomate body with primitive gut, primitive mouth, and a double body-cavity, but no chorda. This embryonic form, the *heterocoelomate* (Fig. 8), may in turn be regarded as the ontogenetic reproduction (induced by heredity) of an ancient ancestral form of the chordons, the *Coleomata* (cf. Chapter XX).

In heterocoelomate amphioxus-like animals the two colom-pouches (presumably gonads or vegetal glands) are separated by a complete median partition, the dorsal and ventral myomere (Figs. 20 (d) and (e)), but in the chordons only the upper part of this ventral partition is maintained, and forms the dorsal myomere. This myomere afterwards takes the form of a ring membrane, which fastens the ventral tube to the chorda (or the ventral colom). At the under side of the ventral tube the colom-walls blend together, until either the median walls break down and disappears. The body-cavity then forms a single ample hollow, in which the gut is quite free, or only attached to the dorsal wall by means of the myomere.

The development of the body-cavity and the formation of the chorda in the higher vertebrates is, like that of the gastrula, clearly modified by the pressure of the food-yolk on the embryonic structures, which forces its blander part into

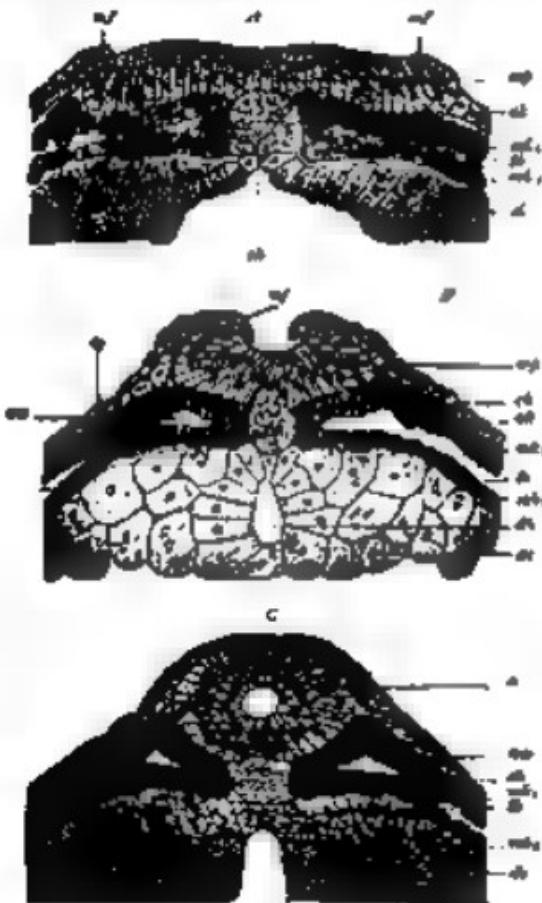


FIG. 21. A, B, C.—Vertical section of the dorsal part of three brachiocephalopsids. (From Herreman.) In Fig. A the ventral border of the involucrum splits larger nerves in Fig. B they cross transversely each other, in Fig. C they meet and form the myomere tube, and finally pass into myomere walls, or myomere of dorsal, & body-cavity walls, and only prevent such a pressure of dorsal, & segment, ventral, & exterior structures as follows, as follows,

a discoid expansion. These congeneric modifications seem to be so great that until twenty years ago these herpetopterous protozoans were totally misunderstood. It was generally believed that the body-cavity in man and the higher vertebrates was due to the division of a simple middle layer, and that the latter arose by cleavage from one or both of the primary germinal layers. The truth was brought to light at last by the comparative embryological research of the Hertwigs. They showed in their *Crown Theory* (1881) that all vertebrates are true ectomeses, and that in every case a pair of column-pouches are developed from the primitive gut by folding. The eumetameric character-forms of the craniates must therefore be derived from the palaeogenetic embryology of the amphioxus in the same way as I had previously proved for the gnathostomes.

The chief difference between the development of the actiniae (amphioxus) and the other vertebrates (gnathostomes) is that the two column-fields of the primitive gut in the former are from the first hollow vesicle, filled with fluid, but in the latter are empty pouches, the layers of which (inner and outer) close with each other. In common parlance we will call a pouch or pocket by that name, whether it is full or empty. It is different in anatomy. In some of our embryological literature rudimentary bags do not count for very much. In mine of the mammals and large fructans on this subject it is proved that vesicles, pouches, or sacs deserve that name only when they are inflated and filled with a clear fluid. When they are not so filled (for instance, when the primitive gut of the gnathostome is filled with yolk, or when the walls of the empty column-pouches are pressed together), these vesicles need not be sacs any longer, but "void structures."

The accumulation of blood-yolk in the ventral wall of the primitive gut (Figs. 52, 53) is the simple cause that converts the flat-shaped column-pouches of the actiniae into the leaf-shaped column-pouches of the craniates. To convince yourself of this, we need only compare with Hertwig's the palaeogenetic conditions of the amphioxus (Figs. 50, 51) with the corresponding congeneric form of the amphibia (Figs. 54-56), and contrast the simple diagram that connects the two (Figs. 57, 58). If we

imagine the ventral half of the primitive gut-wall in the amphioxus embryo (Figs. 57-58) dissected with food-yolk, the ventral column-pouches ( $\beta\beta$ ) must be pressed together by this, and forced to extend to the shape of a thin double plate between the gut-wall and body-wall (Figs. 56, 57). This extension follows a downward and forward direction. They are now directly connected with these two walls. The real unknown connection between the two middle layers and the primary germ-layers is found right at the back, at the margin of the primitive mouth (Fig. 57 a). At this important spot we have the source of embryonic development (Hertwigg), or "zone of growth," in which the conformation (and also the gastrulation) originally proceeds.

Hertwig even succeeded in showing, in the ectomesic embryo of the water salamander (*Triturus*), between the first structures of the two middle layers, the role of



FIG. 57.—Transverse section of the amphioxus embryo of about four millimetres in diameter. (From Hertwig.) A horizontal transverse section, showing the  $\beta\beta$  and  $\gamma\gamma$  layers of cells.  $\beta\beta$  middle layer, of which the ventral (inner) part of the middle layer (middle part of the mid-dorsal-mesoderm) is here folded over to form a dorsal plate, thus dividing the body-cavity of amphioxus.

the body-cavity, which is represented in the diagrammatic transverse section (Figs. 57-58). It arises both through the primitive mouth itself (Fig. 58 a) and, in front of it (Fig. 58 b) the two middle layers ( $\beta\beta$  and  $\gamma\gamma$ ) diverge from each other, and divide the two body-cavities as narrowish slits. At the primitive mouth itself (Fig. 58 a) we can perceive how these form without. It is only here at the border of the primitive mouth that we can show the direct transition of the two middle layers into the two hindmost layers or primary germinal layers.

The structure of the crown also shows the same features in these ectomesic embryos of the amphibia (Fig. 51) as in the amphioxus (Figs. 59-61). It arises from the anterolateral cell-trunk, which forms the width dorsal line of the primitive gut, and occupies the space between the flat column-pouches (Fig. 51 d).

While the nervous canals are formed later in the middle line of the back and separated from the ectoderm as "medullary tube," there takes place at the same time, directly underneath, the separation of the chorion from the ectoderm (Fig. 92 A, B, C). Under the chorion is formed (out of the ventral ectodermic half of the gastrula) the permanent gut, or visceral cavity (*entoderm*) (Fig. 92 D, E). This is done by the convergence, under the rhomb in the median line, of the two dorsal side-borders of the gut-gland-layer (*epib.*), which were previously separated by the chorda-plate (Fig. 92 A, B); these now alone form the clothing of the visceral cavity (*epib.*) (*entoderm*, Fig. 92 C). All these important modifications take place at first in the fore or headpart of the embryo, and spread backwards from there; here at the hinder end, the region of the primitive mouth, the posterior border of the mouth (or *prostomium*)

possible as a matter of fact; even the older illustrations showed no essential identity of features. Thus forty years ago Kolliker gave, in the first edition of his *Histochemistry* (1861), some sections of the chicken-embryo, the features of which could at once be reduced to those already described and explained in the sense of Hertwig's *coelom-thesis*. A section through the embryo in the hatched hen's egg towards the close of the first day of incubation shows in the middle of the dorsal surface a broad ectodermic medullary groove (Fig. 93 R 1), and underneath the midline of the chorion (ab.) and at each side of it a couple of broad mesodermic layers (ep.). These enclose a narrow space or cleft (verb.), which is nothing else than the structure of the body-cavity. The two layers that enclose it—the upper parietal layer (ep.) and the lower visceral layer (ep.)—are pressed together firm without, but clearly durin-



FIG. 93.—Transverse sections of the ventral surface of a very young hen's egg at the end of incubation. (From KOLLIKER.) A horizontal line through the middle of the body-cavity, and passing through the median line of the gut-gland-layer, the epiblast-layer, and the proctodaeum, marks the line of the section. ab., the chorion; ep., the epiblast-layer; verb., the body-cavity; gut-gland-layer, the gut-gland-layer.

remains for a long time the source of development or the zone of fresh construction, in the further building-up of the organism. One has only to compare carefully the illustrations given (Figs. 92-95) to see that, as a fact, the ontogenetic colonization of the amphibia can be deduced directly from the polymorphic form of the nervous (Figs. 29-34).

The same principle holds good for the amniotes, the reptiles, birds, and mammals, although in this case the processes of colonization are more modified and more difficult to identify as a result of the colossal accumulation of food-yolk and the corresponding notable flattening of the germinal disk. However, as the whole group of the amniotes has been developed at a comparatively late date from the class of the amphibia, their colonization must also be directly analogous to that of the latter. This is readily

genuine. This is even clearer a little later, when the medullary furrow is closed into the nerve-tube (Fig. 93 M).

Special importance attaches to the fact that here again the four secondary germinal layers are already sharply distinct, and widely separated from each other. There is only one very restricted area in which they are connected, and actually pass into each other; this is the region of the primitive mouth, which is contracted in the amniotes into a dorsal longitudinal cleft, the primitive groove. Its two lateral side-borders form the *prostomere streak*, which has long been recognized as the most important embryonic source and starting-point of further processes. Sections through this primitive streak (Figs. 94 and 95) show that the two primary germinal layers grow at an early stage (in the shield-gastrula of the chick, a few hours after incubation) into the primitive

streak (*x*), and that the two middle layers extend outward from this thickened axial plate (*y*) to the right and left between the former. The plates of the coelom-layers, the parietal stem-fibre-layer (*m*) and the visceral gut-fibre-layer (*f*), are seen to be still pressed close together, and only diverge later to form the body-cavity. Between the inner borders of the two flat coelom-pouches lies the chorion (Fig. 95 *x*), which here again develops from the midline line of the dorsal wall of the primitive gut.

Coloration takes place in the vertebrates in just the same way as in the birds and reptiles. This was to be ex-

pected, since secondary germinal layers consist of a single stratum of cells.

Finally, we must point out, as a fact of the utmost importance for our anthropogeny and of great general interest, that the hind-end of man has just the same construction as that of the rabbit (Fig. 96). A vertical section that Count Syms made through the primitive mouth or streak of a very young human germinal disk (Fig. 97) clearly shows that here again the four secondary germinal layers are incomparably connected only at the primitive streak, and that here also the two flattened coelom-pouches (*m*) extend outward to right and left from



FIG. 95.



FIG. 96.

Figs. 95 and 96.—Transverse sections of the primitive streak formation stage of the chick embryo at a few hours after the commencement of incubation. Fig. 95 is a longitudinal view of the embryo at a few hours after the commencement of incubation; the primitive streak, or axial plate of each of four germinal layers, and 3 pouches of the coelom, a region of the liver-primitive kidney.

perted, as the characteristic gastrulation of the mammal has descended from that of the reptiles. In both cases a distinct gap exists with primitive streak arises from the segmented ovum, a two-layered germinal disk with long and much thicker primitive streak. Here again the two primary germinal layers are only directly connected (Fig. 96 *mf*) along the primitive streak (at the folding-point of the blastoderm), and from this spot (the border of the primitive mouth) the middle germinal layers (*m*) grow out to right and left between the preceding. In the fine illustration of the caecum of the rabbit which Van Beekdonk has given us (Fig. 98) one can clearly see that each of the

primitive mouths between the older and newer germinal layers. In this case, too, the middle germinal layer consists from the first of two separate strata of cells, the parietal (*m<sub>p</sub>*) and visceral (*m<sub>v</sub>*) mesophylloids.

These important results of the best recent investigations (which have been confirmed by the observations of a number of scientists, I have not enumerated) prove the unity of the vertebrate stem in point of coloration, no less than of gastrulation. In both respects the invertebrate amphioxus—the sole survivor of the accipitres—is found to be the original model that has preserved for us in palaeontological form by a function tardily

most important embryonic processes. From this primary model of oviparousness we can endogenetically deduce all the embryonic forms of the other vertebrates, the craniota, by secondary modifications. My thesis of the universal formation of the gastrula by folding of the blastula has now been clearly proved for all the vertebrates; so also has been Hertwig's thesis of the origin of the middle germinal layers by the folding of a couple of epiblastic pouches which appear at the border of

typical, unsegmented, worm-like form, which has an axial chorda between the dorsal nerve-tube and the ventral gut-tube. This instructive chorda (Figs. 33-36) provides a valuable support of our phylogeny; it indicates the important moment in our stem-history at which the stem of the chordonians (tunicata and vertebrates) parted far over from the divergent stems of the other metazoa (annelines, arachnida, and molluscs).

I may express first my opinion, in the



FIG. 33.—Transverse section of the primitive embryo (or primitive model) of a rabbit. (From Korschelt.) An epiblastic model of type of *Chondro-mesoblast*, or *an* = outer and *ar* = inner germinal layers, and *mb* = mesoblast, *m* = *metabolism*, *ep* = epiblastic layer, see 'second layer' of the embryo.



FIG. 34.—Transverse section of the primitive gastrula (or primitive model) of a dogfish embryo (or the amphioxus). (From Chant 1926.) An epiblastic model, or type of *meso-mesoblast*, *an* = outer and *ar* = inner germinal layers, *mb* = mesoblast, *m* = *metabolism*.

the primitive mouth. Just as the gastron-thesis explains the origins and identity of the two primary layers, so the endo-theory explains those of the four secondary layers. The point of origin is always the primitive mouth of the gastrula, at which the two primary layers pass directly into each other.

Moreover, the evidence is important on the immediate birth of the chorda, the embryonic reproduction of the an-

terior of a chordon-theory, that the characteristic chorda-lure of the chordonians in reality has great significance—it is the typical reproduction (preserved by heredity) of the simplest common stem-form of all the vertebrates and tunicates, the long-extinct *Clypeomorpha*. We will return in the twentieth chapter to these worm-like ancestors, which stand out as luminous points in the obscure stem-history of the invertebrates ancestors of our race.

## CHAPTER XL.

## THE VERTEBRATE CHARACTER OF MAN

We have now secured a number of firm standings-points in the labyrinthine course of our individual development by our study of the important embryological forms which we have called the cysts, metas, blastula, gastrula, ectoblast, and chordula. But we have still in front of us the difficult task of discerning the complicated frame of the human body, with all its different parts, organs, members, &c., from the simple form of the chordula. We have previously considered the origin of this four-layered embryo from the two-layered gastrula. The two primary germinal layers, which form the entire body of the gastrula, and the two middle layers of the ectoblast, that develop between them, are the four simple ectodermata, or epithelia, which alone go to the formation of the complex body of man and the higher animals. It is so difficult to understand this construction that we will find some companion who may help us out of many difficulties.

The helpful associate is the science of comparative anatomy. Its task is, by comparing the fully-developed bodily forms in the various groups of animals, to learn the general laws of organization according to which the body is constructed. At the same time, it has to determine the affinities of the various groups by critical appreciation of the degrees of difference between them. Formerly, this work was concerned in a teleological sense, and it was sought to find traces of the plan of the Creator in the actual purposeful organization of animals. But comparative anatomy has gone much deeper since the establishment of the theory of descent; its philosophical aim now is to explain the variety of organic forms by adaptation, and their unity by heredity. At the same time, it has to recognize in the shades of difference in form the degree of blood-relationship, and make an effort to reconstruct the ancestral tree of the animal world. In this way, comparative anatomy comes into the closest relations with comparative

embryology on the one hand, and with the science of classification on the other.

Now, when we ask what position man occupies among the other organisms according to the basic teaching of comparative anatomy and classification, and also man's place in the zoological system is determined by comparison of the various bodily forms, we get a very definite and significant reply, and this reply gives us extremely important conclusions that enable us to understand the embryological development and its evolutionary progress. Since Cuvier and Baer, since the former's progress that was effected in the early decades of the nineteenth century by these two great zoologists, the opinion has generally prevailed that the whole animal kingdom may be distributed in a small number of great divisions or types. They are called types because a certain typical or characteristic structure is commonly preserved within each of these large sections. Since we applied the theory of descent to this doctrine of types, we have learned that this common type is an outcome of heredity; all the animals of one type are blood-relatives, or members of one stem, and can be traced to a common ancestral form. Cuvier and Baer set up four of these types: the vertebrates, articulate, mollusk, and radiata. The first three of these are still recognized, and may be conceived as natural phylogenetic groups, or phyla in the sense of the theory of descent. It is quite otherwise with the fourth type—the radiata. These polyps, hitherto known as yet at the beginning of the nineteenth century, were made to form a sort of brother-sisters, two of which were cast all the lower animals that did not belong to the other three types. As we obtained a closer acquaintance with them in the course of the last fifty years, it was found that we must distinguish among them from five to eight different types. In this way the total number of animal stems or phyla has been raised to eight or twelve (cf. Chapter XX.).

There twelve classes of the animal kingdom are, however, by no means co-ordinated and independent types, but have definite relations, partly of subordination, to each other, and a very different phylogenetic history. Hence they need not be arranged simply in a row one after the other, as was generally done until thirty years ago, and as still done in some systems. We must discriminate them in three independent principal groups of very different values, and arrange the vertebrates phylogenetically on the principles which I laid down in my *Development of the Embryo*, and developed in the *Study of the Creative Theory*. We have first to distinguish the invertebrate animals (*protozoa*) from the metazoan-like *invertebrates* (*echinoderms*). Only the latter exhibit the important process of segmentation and gastrulation, and they also have a primitive gut, and form genuine larval stages.

The metazoa, the coelomate organisms, then subdivide into two main divisions, according as a body cavity is or is not developed between the primary germinal layers. We may call these the *coelomates* and *acelomates*. The former are often also called *metazoans* or *metameric*, and the latter *inmetazoans*. This division is the more important as the acelomates (without coelom) have no blood and blood-vessels, nor no gills. The coelomates (with body-cavity) have generally at least, and blood and blood-vessels. These are first class belonging to the *echinoderms*: the *echinoderms* ("gracile-metazoans"), *echinoids*, *cnidaria*, and *annelids*. Of the coelomates we can distinguish at present: the *annelids* at the bottom represent the common *metazoa* derived from the protostomes; the other five typical classes of the coelomates—the *molluscs*, *arthropods*, *echinoderms*, *fishes*, and *vertebrates*—being derived later there.

Next is, in his whole structure, a true vertebrate, and develops from an unsegmented ovule in just the same characteristic way as the other vertebrates. They are no longer by the right-hand standard the fundamental fact, nor of the fact that all the vertebrates form a unified phylogenetic unity, a single class. The whole of the members of this class, from the amphioxus and the cyclostomes to the apes and man, have the same characteristic organization, structure, and development of the central nervous, and also in the

same way from the anterior embryonic form of the cerebrum. Without going into the difficult question of the degree of this class, we must emphasize the fact that the vertebrate class has no direct affinity whatever to five of the other ten classes: these five animal phyla are the *spiroglosa*, *annelids*, *molluscs*, *echinoderms*, and *arthropods*. On the other hand, there are important and, to my mind, even phylogenetic relations to the other ten: the *molluscs* (through the *annelids*), the *gnathophaea* (through the *annelids* and *gnathophores*), the *fishes*, and *vertebrates* (through the *annelids*), and the *insects* (through the *annelids*).

Now we are to explain these phylogenetic relations in the present state of our knowledge and to try to interpret in the vertebrates the earliest vertebral mass, will be discussed later (Chapter XII). For the present our task is to make明白 the vertebrate character of man, and especially to point out the chief characteristics of organization by which the vertebrate class is profoundly separated from the other seven classes of the animal kingdom. Only after these comparative-anatomical considerations shall we be in a position to attack the difficult questions of our embryology. The development of even the simplest and lowest vertebrates gives the unique cerebrum (Figs. 11, 12) so complicated and difficult to follow that it is necessary to understand the organization of the fully-formed vertebrate in order to grasp the course of its embryological evolution. But it is equally important to realize our situation, in this general comparative description of the vertebrates, to the empirical facts, and then by all the theoretical. Hence, in giving our general anatomical description of the chief features of the vertebrates and their organized organization, I want all the sufficient facts, and material say well to the most important characteristics.

Most of course, will seem to the reader to be evident that in unity of metabolism and secondary relation, he does not participate at all in the life of unsegmented protists and metazoozoa. For instance, the head and vertebral column, and the embryo as are non-participated in the nervous. It is true that these parts are very important phylogenetically; but for the empirical biological conception of the vertebrates they are not essential, because they are only found in the Molluscs, not the lower, *insects*. The lowest vertebrates have

either shell nor vertebral, and no notochord or body. Even the human embryo passes through a stage in which it has no shell or vertebral; the trunk is quite simple, and there is yet no trace of brain and legs. At this stage of development man, like every other higher vertebrate, is essentially similar to the simplest vertebrate form, which we now find in only one living specimen. This one lowest vertebrate that marks the clearest stage—undoubtedly the most interesting of all the vertebrates after man—is the famous lancelet or amphioxus, to which we have already often referred. As we are going to study it more closely later on (Chapters XVI and XVII), I will only make one or two passing observations on it here.

The amphioxus lies buried in the sand of the sea, in about one or two inches of depth, and has, when fully developed, the shape of a very simple, longish, lanceolate leaf; hence its name of the lancelet. The narrow body is compressed on both sides, almost equally passed at the free and fixed ends, without any trace of external appendages or articulations of the body with head, neck, breast, abdomen, etc. In what shape it is simple that the first dove ever thought it was a salmón trout. It had not until much later—half a century ago—that the tiny creature was studied more carefully, and was found to be a true vertebrate. Many recent experiments have shown that it is of the greatest importance in correlating with the comparative anatomy and physiology of the vertebrates, and therefore with human physiology. The amphioxus provides the great source of the origin of the vertebrates from the invertebrates, and in its development and structure connects directly with certain lower invertebrates, the molluscs.

When we make a median section of the body of the amphioxus, thereby cutting longitudinally through the whole body from end to end, and similarly transversely across from right to left, we get anatomic portions of the same in definiteness (cf. Figs. 48-50). In the brain they correspond to the skull which we have, with the aid of comparative anatomy and embryology, of the primitive type or build of the vertebrates—the long anterior form to which the whale also shows its origin. As we take the physiologic history of the vertebrates down to the simplest stages, and among a

series from a primitive condition for all the vertebrates, from amphioxus to man, we are justified in forming a double hypothesis. One of this primitive vertebrate of *Protophydæa* or *Vertebræa*. We need only recognize a few slight and immaterial changes in the real nature of the amphioxus in order to have this ideal anatomic figure or diagram of the primitive vertebrate form, as we see it in Figs. 48-50. The amphioxus depicts a little more this primitive form than we see in a certain man, described as a "peculiar" primitive vertebrate."

The main form of our hypothetical primitive vertebrates was at all events very simple, and probably more or less similar to that of the lancelet. The lanceolate body is straight and unsegmented at the sides (Figs. 48-50), and in section (Figs. 50, 501). There are no segmental articulations and no segmental appendages, in the shape of limbs, legs, or fins. On the other hand, the division of the body into the anterior head and neck, two probably clearer in *Protophydæa* than it is in the unchanged amphioxus, the development in both halves the left or head-half of the body contains different organs from the right, and different on the dorsal from the ventral side. As this important division is found in so in the sea-shore, the amphioxus, derivatives of vertebrates, we may suppose that it was also found in the prochordians, the common ancestors of both classes. It is also very pronounced in the young larvae of the cyclostomes; this fact is particularly interesting, as this paleozoic larva third, or in other respects also an important connecting link between the higher vertebrates and the worms.

The head of the nervous, or the anterior half of the body (both of the rest apertures and the head prosopoduct), contains the branched (proto) gut and heart in the ventral section and the brain and nervous-organs in the dorsal section. The trunk, or posterior half of the body, contains the hepato-gut and nervous-

\* The third figure of the vertebrates is given in Fig. 48, as a hypothetical diagram of the amphioxus, clearly indicated as the head of the amphioxus, but with a series of short hypopophyses or notochordal processes and appendages on the ventral side of the prochordous and aperturous side. The figure is given to show the probable connection of the amphioxus with the vertebrates, and the probable connection of the amphioxus with the prochordous forms.

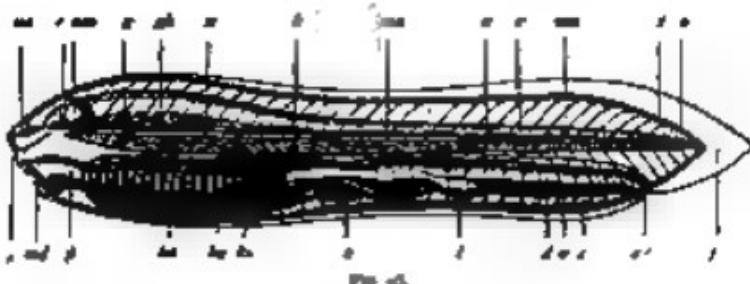


FIG. 45.



FIG. 46.



FIG. 47.



FIG. 48.

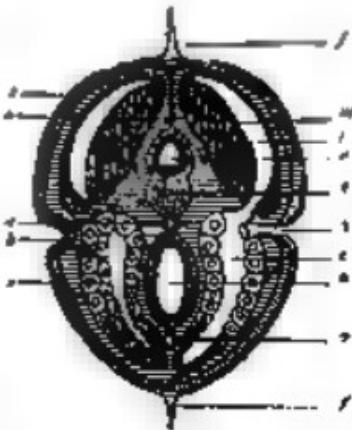


FIG. 49.

FIG. 45-49.—The blood vessels, nephridia, &c., of the leech (*Hirudo medicinalis*). Diagrams from the work of Dr. G. H. Verrill, U.S.N.M., New Haven, 1886, pp. 716, 717, 720, 721, Fig. 45, transverse section through the head; Fig. 46, through the pharynx, to the first or the last through the proventriculus, to the rectum, through the pharynx; Fig. 47, transverse section of the trunk; in the right a ventral view is shown, a dorsal view, on top. A lateral view, showing the nervous system, &c., is shown below. The figures show the nervous system, &c., the border of the skin, a large coelomic cavity, the rectum, the pharynx, the oesophagus, the gizzard, the stomach, the mouth,

glide in the ventral part, and the spinal marrow and nerve of the medulla in the dorsal part.

In the longitudinal section of the living vertebrates (Fig. 59) we have in the middle of the body a thin and flexible, but stiff, cylindrical rod, pointed at both ends (*spine*). It runs the whole length through the middle of the body, and forms, as the central vertical axis, the original structure of the later vertebral column. This is the spinal rod, or *vertebral column*, also called *spinal axis*, *vertebral canal*, *spinal canal*, *dorsal canal*, *vertebral duct*, or, briefly, *spine*. The spine, but flexible and viscid, is made up of a cartilaginous mass of cells, and forms the lateral axial skeleton, or central frame of the body; it is only found in vertebrates and annelids, and is very often wanting. As the first structure of the spinal column it has the same radial segmentation in all vertebrates, from the amphioxus to man. But it is only in the amphioxus and the cyclostomes that the spinal rod remains its simplest form throughout life. In man and all the higher vertebrates it is found only in the earlier embryonic period, and is afterwards replaced by the articulated vertebral column.

The spinal rod or *spine* is the real solid chief axis of the vertebrate body, and of the crew there corresponds to the spinal ligament, and serves to direct us with some confidence in the orientation of the principal organs. We therefore take the vertebrate-body in its original, central disposition, in which the long-axis lies horizontally, the dorsal side upward and the ventral side downward (Fig. 59). When we make a vertical section through the whole length of the long axis, the body divides into two equal and symmetrical halves, right and left. In each half we have apparently the same organs in the same disposition and connection; only their direction is related to the vertical plane of section, or median plane. It is easily reversed, the left half is the reflection of the right. We call the two halves *anterior* and *posterior*. In the median plane of section that divides the two halves the median ("median") axis, or "dorsiventral axis," goes from the head to the body, corresponding to the sagittal plane of the skull. But when we make a horizontal longitudinal section through the chord, the whole body divides into a dorsal and a ventral half. The line of section that passes through

the body from right to left is the transverse, frontal, or *lateral axis*.

The two halves of the vertebrate body that are separated by this horizontal transverse axis and by the median longitudinal character, the dorsal half is mostly the animal part of the body, and comprises the greater part of what are called the animal organs, the nervous system, muscular system, excretory system, etc.—the instruments of movement and nutrition. The ventral half is essentially the vegetative half of the body, and comprises the greater part of the vertebrate's vegetal organs, the vegetal and vascular systems, sexual organs, etc.—the instruments of nutrition and reproduction. Hence in the construction of the dorsal half it is mainly the spine, and in the construction of the ventral half mainly the liver, provided before that is developed. Each of the two halves develops in the shape of a tube, and encloses a cavity in which another tube is fixed. The dorsal half contains the narrow spinal-canal cavity or vertebral canal above the shield, in which lies the tubular-shaped neural nervous system, the medullary tube. The ventral half contains the much more spacious ventral cavity or body-cavity underneath the shield, in which are fixed the alimentary canal and all its appendages.

The medullary tube, as the neural nervous system or psychic organ of the vertebrates is called at its first stage, consists, in man and all the higher vertebrates, of two distinct parts: the large brain, contained in the skull, and the long spinal cord which stretches from there over the whole dorsal part of the body. Even in the primitive vertebrates this composition is plainly indicated. The fore half of the body, which corresponds to the head, encloses a brain-shaped vesicle, the brain (Fig. 60), this is prolonged backwards into the thin cylindrical tube of the spinal marrow (Fig. 61). Hence we find here the very important psychic organ, which accomplishes motion, will, and thought, in the vertebrates, so its simplest form. The thick wall of the nerve-fibres which run through the long axis of the body immediately over the spinal rod, contains a narrow central canal filled with fluid (Fig. 61, *pt. 10*, *r.*). We still find the medullary tube in this very simple form in the embryo of all the vertebrates, and it remains this form in the amphioxus throughout life;

only in the latter does the cylindrical mandibular tube bend sideways. On separation of brain and spinal cord, the buccal's mandibular tube runs nearly the whole length of the body above the spine, in the shape of a long thin tube of almost equal diameter throughout, and there is only a slight swelling of a slight at the front to represent the outline of a cervical loop. It is probable that this peculiarity of the construction is connected with the partial autonomy of its head, as the cervical loop at the one hand and the young epibranchial on the other clearly show a division of the epibranchial head, moreover, from the viscerum, including spinal marrow.

Presently, as most men in the same stage begin to cause the definitive stages of the various organs of the epibranchium, which we will describe later (Chapter XVI) Preparatory, on the other hand, probably had three pairs of epibranchia, though of a simple character, a pair of, or a single auditory apparatus, right in front (Fig. 50, pp. 90-91), a pair of eyes (Fig. 52) in the lateral walls of the head, and a pair of simple respiratory cavities (Fig. 53) behind. There was also, perhaps, a single parotid or "placed" eye at the top of the chief epibranchium, &c.

In the cervical median plane (or middle plane, dividing the buccal body into right and left halves) we have to the anterior, underneath the rhomb., the visceromotor and cerebral tubæ, and above it the mandibular tubæ, and above it the hypobranchial partition of the two halves of the body. With this partition is connected the root of epibranchial band which runs as a thick band to the mandibular tube and the visceromotor tubæ, and is, therefore, called the third-shield (prosopothrix). It originates from the dorsal and ventral part of the visceromotor, which we shall call the visceromotor plate or "viscerum" — the definitive embryo. In the latter the chief part of the viscerum — the visceromotor column and shield — develops from this chord-shield; in the nervous trunks no muscle form, no a soft connective tissue, from which are formed the membranous partitions between the various muscular plates or myotomes (Figs. 50, 59, 90).

To the right and left of the viscerum, at each side of the mandibular tube and the underlying spinal rod, we find in all the vertebrates the large mass of muscle that constitutes the musculature of the

trunk and skull. Its musculature, although there are very substantially differentiated and connected in the developed vertebrates (corresponding to the various parts of the body skeleton), is yet (and primitive vertebrates we can distinguish only two pairs of these principal muscles, which run the whole length of the body parallel to the rhomb. These are the upper (dorsal) and lower (ventral) lateral muscles of the trunk. The upper (dorsal) muscle, or thoracine and dorsal muscle (Fig. 50, 90), forms the thick mass of flesh on the back. The lower (ventral) muscle, or the ventral muscle of the body, forms the fleshy wall of the abdomen. Both sets are segmented, and consist of a double row of muscular plates (Figs. 50, 90, 91), the number of these myotomes determining the number of joints in the trunk, or abdomen. The myotomes are the divisions from the thick wall of the epibranchia (Fig. 50, 91).

Outside this muscular robe we have the covered surface of the vertebrate body, which is known as the cutis or skin. This strong red skin contains connective tissue, in its deeper parts, chiefly of fat and loose connective tissue, and in the upper layers of muscular muscles and former connective tissue. It covers the whole surface of the fleshy body, and is of considerable thickness in all the vertebrates. But in the serous the serous is merely a thin plate of connective tissue, or unmyotomized "visceralplate" (fascia vera, Figs. 50-52).

Immediately above the serous is the outer skin (epidermis, &c.), the general covering of the adult outer surface. In the higher vertebrates the hair, scales, feathers, claws, scales, etc., grow out of this epidermis. In man, with all the appendages and products, of simple cells, will be the glands, etc. Its cells are connected with the invaginations of the nervous nerves. Originally, the outer skin is a perfectly simple covering of the outer surface of the body, composed only of homogeneous cells — a plasmatic membrane. In this simplest form, as a thin-layered epithelium, we find it, at first, in all the vertebrates, and throughout life in the serous. It afterwards grows thicker in the higher vertebrates, and divides into two-layers — an outer, being connective-tissue layer and an inner, outer nervous layer — and a number of external and internal appendages grow out of it; naturally, the hair, nails, claws, etc., and

invariably, the mouth-glands, the glands, etc.

It is probable that in our primitive vertebrates the skin was related in the middle line of the body to the shape of a vertical furrow (*ff.*). A similar furrow goes round the greater part of the body, it is found to-day in the amphioxus and the cyclostomes; we also find one in the tail of fish-larvae and tadpoles.

Now that we have considered the external parts of the vertebrates and the internal organs, which mostly lie in the dorsal half, above the chorda, we turn to the regional organs, which lie for the most part in the ventral half, below the spinal cord. Here we find a large body-cavity or coelomic cavity in all the classes. The coelomic cavity that contains the greater part of the viscera corresponds to only a part of the original coelome, which we consider as the neck-chamber; hence it may be called the *coelomocystis*. As a rule, it is still briefly called the coeloma; however it was known in anatomy as the pharyngocoeloid cavity, because and the other mammals (but only in these) the coeloma, slender, more fully developed, into two different cavities, which are separated by a transverse partition—the diaphragm. The fore or pectoral cavity (*pseudo-cavity*) contains the mouth-glands (gullet), heart, and lungs; the liver, or peritoneum, or abdominal cavity contains the stomach, small and large intestines, liver, rectum, bladder, etc. But in the cyclostomes, before the mouth-glands are developed, the two cavities form a single anterior body-cavity, and up to the time at all the body-coelome disappears through the life. The body-cavity is divided into a distinct layer of cells, the *mesothelium*. In the embryo the coelom is augmented both dorsally and ventrally, so that vertebrate protozoa and primitive genital organs plainly show (Fig. 10).

The chief of the viscera in the body-cavity is the alimentary canal, the organ that represents the whole body in the gastrula. In all the vertebrates it is a long tube, enclosed in the body-cavity and thick or less differentiated in length, and has two apertures—a mouth for taking in food (Figs. 10, 102, 103) and an ure for the excretion of excretory wastes or excrements (*uf.*). With the alimentary canal a number of glands are connected which are of great importance for the vertebrates body, and which all grow out of the

coel. Glands of this kind are the salivary glands, the lung, the liver, and many other glands. Nearly all these glands are situated in the ventral, probably there were recently a couple of simple lymphatic tubes (Figs. 10, 102) in the vertebrate medulla. The wall of the alimentary canal and all its appendages consists of two different layers; the inner epithelial lining is the gut-glandular-layer, and the outer, fibrous envelope consisting of the gut-fibre-layer; it is mainly composed of muscle-fibres which accomplish the digestive movements of the canal, and of connective-tissue fibres that form a firm envelope. We have a continuation of it in the epibranchial, a thin, longitudinal layer, by means of which the alimentary canal is fastened to the ventral side of the chorda, especially the dorsal portions of the two epibranchial-processes. The alimentary canal is very much modified in the vertebrates both as a whole and in its several sections, though the original structure is always the same, and is very simple. As a rule, it is longer (than several times longer) than the body, and therefore twisted and winding within the body-cavity, especially at the lower end. In man and the higher vertebrates it is divided into several sections, when represented by valves—the mouth, pharynx, oesophagus, stomach, small and large intestine, and rectum. All these parts develop from a very simple structure, which originally (throughout life in the amphioxus) runs from end to end under the chorda in the shape of a straight cylindrical canal.

As the alimentary canal may be regarded morphologically as the older and more important organ in the body, it is becoming so understood its evolution is in the vertebrates more fully, and distinguishes them from unvertebrate forms. In this connection we must particularly note that the alimentary canal of every vertebrate shows a very characteristic division into two sections—a fore and a hind division. The fore division is the head-gut or branched gut (Figs. 10, 102, 103), and is closely connected with respiration. The hind section is the long-gut or hepato-gastric apparatus—digestion, *etc.*, *etc.* In all vertebrates there are formed, at an early stage, to the right and left in the fore-part of the head-gut, certain special cells that have an intimate connection with the original respiratory apparatus of

the vertebrates—the bivalved (gill) shells (*A.*). All the lower vertebrates, the cephalopods, bony-fishes, and sharks are externally breathing in virtue of the gills, and letting it out again by the bivalved shells of the gills. This power comes by breathing. The oxygen consumed is supplied by the blood-vessels, which spread out on the gills throughout the gill-shells, the pectoral-shells (*A.*). These very characteristic bivalved shells and vessels are found in the embryo of man and all the higher vertebrates at an early stage of development, just as we find them throughout life in the lower vertebrates. However, these shells and vessels never become respiratory organs in the embryo, birds, and reptiles, but gradually develop into quite different parts. First, the fact that they are found at first in the embryo seems as to the fishes to me one of the most interesting proofs of the degree of their three higher classes than the fishes.

Not less interesting and important is an organ that develops from the ventral wall in all vertebrates—the thymus or hypopharyngeal gland. In the embryo and the ovaries it appears throughout the body of a glandular-filamentous growth, which runs down from the mouth, in the ventral midline line of the gill-gut, and collects small particles of food to the surface (Fig. no. 4). But in the embryo the thyro-thymus (thyro-thymus), so developed from it, the gland thus lies in front of the larynx, and which, when comparatively enlarged, forms great *swellings*.

From the beginning we get not only the gills, the organs of water-breathing in the lower vertebrates, but also the lungs, the organs of atmospheric breathing in the five higher classes. In these cases a vascular field appears in the gills of the embryo at an early stage, and gradually takes the shape of two spacious sacs, which are afterwards filled with air. These are the two air-breathing lungs, which take the place of the water-breathing gills. But the vascular arrangement, from which the lungs arise, is simply the branching air-tube vessels, which we call the branching-vessels of the lung, and which allow the specific respiration, acting as hydrostatic organs or filtering apparatus. This structure is not found in the lowest vertebrate classes—the cephalopods and cyclostomes. We shall see more of it in Vol. II.

The second chief centre of the water-breathing, the trunk or thorax, which

respiratory division, is of very simple construction in the embryo. It consists of two different chambers. The first chamber immediately behind the gut, is the expanded stomach (*mes.*); the second, narrower and longer chamber, is the straight small intestine (*du.*) of man twisted on the ventral side by the sacs (*co.*). Near the line of the two chambers in the dorsal cavity we find the liver, in the shape of a simple tube or blind sac (*li.*); in the amniotes it is simple; in the primates it is very probably double (Figs. 48, 102).

Chiefly owing morphologically and physiologically to the embryonic condition of the vascular system of the vertebrates, the chief arteries of which develop from the heart-gland, it consists of two distinct but closely connected parts, the system of blood-vessels and that of lymphatics. In the mesoblast of the tail we find red blood, and in the tail-collecting lymph. To the lymphatic system belongs, first of all, the lymphatic vessels proper or collecting veins, which are distributed among all the regions, and conduct the excess fluid from the tissues, and conduct these into the venous blood; but besides these there are the chyle-vessels, which absorb the white chyle, the milky fluid prepared in the alimentary canal from the food, and conduct this also to the blood.

The blood-vessel system of the vertebrates has a very elaborate construction, but seems to have had a very simple form in the primitive vertebrates, as the first of today, particularly in the metazoa (or insects, molluscs, annelids, and the cephalopods). We accordingly distinguish all of all its essential structural parts of its two large single blood-vessels, which lie in the dorsal wall of the gut, and run along the alimentary canal in the ventral plane of the body, one above and the other underneath the vessel. These primitive vessels give not numerous branches to all parts of the body, and these later ones either by nodes before and behind, or else still then the primitive artery and the primitive vein. The first corresponds to the dorsal vessel, the second to the ventral vessel, of the embryo. The primitive or primitive artery, usually called the aorta (Fig. 51, a), lies above the gut in the middle line of its dorsal side, and conducts arterial or arterial blood from the gills to the body. The primitive or primitive vein (Fig. 51) lies below the

gut, in the middle line of the ventral side, and is therefore also called the *ventral aorta*: it conducts darkened venous blood back from the body to the gills. At the branching points of the gut or from the two ends are excreted by a network of branches, which run in series between the gill-slits. These "branchial muscular arches" (Fig. 1) run along the gillarches and have a direct share in the work of respiration. The anterior commissure of the gills and ventricle runs on the ventral wall of the gut-gill, and gives off three muscular arches upwards, i.e. the branchial artery (Fig. 1). At the border of the two arches of the ventral aorta it enlarges into a smooth, kidney-shaped sac (Figs. 49, no. 2). This is the first cavity of the heart, which above and below a four-chambered pump in the higher vertebrates and man. There is no heart in the amphioxus, probably owing to degeneration. In *prostomia* the ventral gut always probably had the simple form in which we will find it in the ascidæ and the embryo of the crinoids (Figs. 49, no. 2).

The kidneys, which act as organs of excretion or urinary organs in all vertebrates, have a very different and elaborate construction in the various sections of this view; we will consider them further in the hexameric chapter. Here I need only mention that in our invertebrate protostomes they probably had the same form as in the natural amphioxus—the primitive kidneys (*prostomia*). These are originally made up of a double pair of little coeca, which directly cover the ventral jaws or the tips of the hindgut (Fig. 49, no. 1). The lower upper pair of these embryological muscle systems with a colic duct form the body-wall—*the external aperture opens in lateral grooves of the epidermis, a couple of longitudinal grooves in the lateral surface of the outer skin* (Fig. 49, no. 1). The pro-stomach duct is formed by the closing of this groove to the right and left of the sides. In all the crinoids it develops in the early stage in the larva plan: in the amphioxus it seems to be converted after a time into the aorta, or post-embryonic aorta.

Next to the kidneys we have the sexual organs of the vertebrates. In most of the members of this view the two are joined in a single unpaired system. It is only in a few groups that the urinary and sexual organs are separated by the

epiphyses, the cyclostomes, and some members of the fish-class). In view of all the higher vertebrates the sexual apparatus is made up of various parts, which we will consider in the hexameric chapter. But in the two lowest classes of our class, the cyclostomes and cycloformes, they consist merely of simple round glands or gonads, the ovaries of the female and the testes (phallus) of the male; the former provide the ova, the latter the sperm. In the crinoids we always find only one pair of gonads; in the amphibian several pairs, arranged in successive rows. They must have had the same form in our hypothetical *prostomia* (Fig. 49, no. 1). These segmented pairs of gonads are the original ventral halves of the metapleuralia.

The segments which we have now appropriated to this general cavity, and of which we have named the *metapleuralia* division, are those parts of the segments that are found in all vertebrates without exception in the same relation to each other, however much they may be modified. We have already had in view the transverse section of the body (Figs. 101, 102), *because* in this we can most clearly the distinctive arrangement of them. But to complete the picture we must also consider the segmentation of metapleuralia division of them, which has yet been hardly worked, and which is still less in the transverse section. In man and all the more advanced vertebrates the body is made up of a series of sets of similar members, which stand each other in the long axis of the body—the segments or vertebrae of the myomere. In man these homogeneous parts number thirty-three in the trunk, but they run to several hundred in many of the vertebrates (such as serpents or fish). As the internal articulation of vertebrates is mainly found in the vertebral column and the myomeric process, the sections or vertebrae were formerly called *pro-vertebrae*. As a fact, the articulation is by no means strictly determined and caused by the skeleton, but by the muscular system and the segmented arrangement of the kidneys and gonads. However, the connection from these pre-vertebrae or dorsal notochord is usually, and rightly, not derived as a present character of the vertebrates, and the manifold division or differentiation of them is of great importance in the various groups of the vertebrates. But as far as our present

task—the derivation of the single body of the primitive vertebrates from the amphibia—is concerned, the articulate parts or metamers are of secondary interest, and we need not go into them just now.

The characteristic composition of the vertebrate body develops from the embryonic structure in the same way in man

that this answer is just as certain and simple in the case of the origin of man from the mammals. This advanced vertebrate class is also monophyletic, or has evolved from one common stem-group of lower vertebrates (reptiles, and, earlier still, amphibia). This follows from the fact that the mammals are



FIG. 4. R. C. D.—Specimens of mammalian mammary glands and nipples (diaphragm). A. A. of adult individual female (with two nipples on the left above, the breast removed, from a 20-year-old woman, who had had children at least five years before). (From Haeckel.) B. The highest number, the right, young adult. Three years before, over year before, the breast removed by self. From a 15-year-old woman at Würzburg. (From Körber.) C. Three pairs of nipples, two pairs on the normal glands and one pair above, from a 15-year-old Japanese girl. D. Four pairs of nipples, one pair above the normal and two pairs of small secondary nipple rudiments, from a 15-year-old Chinese woman. (From Wiedersheim.)

as in all the other vertebrates. As all competent experts now admit the monophyletic origin of the vertebrates on the strength of this significant agreement, and this "common descent of all the vertebrates from one original monad-form" is admitted as an historical fact, we have found the answer to "the question of questions." We may, whatever point we

choose to distinguish from the other classes of the vertebrates, not merely in one striking particular, but in a whole group of distinctive characters.

It is only in the mammals that we find the skin covered with hair, the breast-cavity separated from the abdominal cavity by a complete diaphragm, and the larynx provided with an epiglottis. The

mammals there have three small mammary buds in the breast—nearly—a feature that is associated with the characteristic modification of their mammary glands. Their red blood-corps have no corpus, whereas that is retained in all other vertebrates. Finally, it is only in the mammals that we find the remarkable formation of the breast structure which has given its name to the whole class—the nursing of the young by the mother's milk. The mammary glands which serve this purpose are interesting in as many ways that we may devote a few lines to them here.

As is well known, the lower mammals, especially those which bear a number of young at a time, have several mammary glands at the breast. Marmosets and apes have five pairs, one pair or five pairs, dogs and jackals four pairs, rats and bears three pairs, most of the primates two pairs, each provided with a tail or nipple (*monkey*). In the various species of the half-apes (*proconsul*) the nipples were a good deal. On the other hand the bats and apes, which only bear one young at a time as a rule, have only one pair of mammary glands, and these are found at the breast, as in man.

These variations in the number of mammae of the mammalian species (*suborder*) have been much investigated in the light of results received in comparative anatomy. It has been shown that in man and the apes as well as the half-apes mammary glands (*Appenstielae*) and corresponding nests (*Appressores*) in both cases (Fig. 103) show but one pair of this kind—*A*, *B*, and *C* of these writers, and *D* of ours. They prove that all the above-mentioned numbers may be found considerably to man. Fig. 103 *A* shows the breast of a Berlin woman who had had children—twelve, three, and who has a pair of small mammary buds (with two nipples on the left side) where the two normal breasts; this is a common occurrence and the small red bud above the breast is not uncommonly represented in ancient statues of Venus. In Fig. 103 *C* we have the same phenomena in a Japanese girl of thirteen, who has two nipples on each breast besides (these prove abridged). Fig. 103 *D* is a case of twenty-five with but one pair of nipples (as in the dog), a small pair above and two small pairs beneath the large normal ones. The

maximum number of five pairs (as in the cow and baboon) was found in a Polish woman of twenty-two who had had seven children; this was given by each nipple; there were three pairs of mammae nipples above and one pair underneath the normal and very large ones (Fig. 103 *A*).

A number of recent investigations (especially among rodents) have shown that these things are not uncommon in the male as well as the female sex. They can only be explained by evolution, which originates them in ovaries and breast-buds. The earlier ancestors of all the primates (including man) were lower primates, which had, like the baboon (one of the oldest forms of the living primates), several mammary glands (five or more pairs) in the abdominal skin. In the apes and man only a couple of them are normally developed, but from time to time we get a development of the unpaired structures. Special notice should be taken of the arrangement of these mammary structures; they form, as is clearly seen in Figs. 103 *A* and *D*, two long rows, which diverge forward towards the arm pit, and converge behind to the middle line (towards the heart). The milk-glands of the polygynous lower primates are arranged in similar lines.

The phylogenetic migration of polygyny, as given in comparative anatomy, has lately found considerable support in anatomy. Hens Schultze, E. Schäfer, and others, have found that there are vestiges in the human embryo at the ninth week (when it is three-fifths of an inch long) the microscopic traces of five pairs of mammary glands, and that they are arranged in regular distances in two lateral and divergent lines, which correspond to the mammary lines. Only one pair of these—the central pair—are normally developed, the others disappearing. Hence there is for a time in the human embryo a normal hypopygium, and this can only be explained by the descent of man from lower primates (apes) with several pairs.

But the anti-gyn of the mammal has a great morphological interest from another point of view. This organ for bearing the young in man and the higher primates is, as is known, found in both sexes. However, it is usually active only in the female sex, and yields the valuable "mother's milk"; in the male sex it is

small and inactive, a real mammary organ of no physiological interest. Nevertheless, in certain cases we find the breast as fully developed in man as in woman, and it may give milk for feeding the young.

We have a striking instance of this gynecomastia (large milk-giving breasts in a male) in Fig. 104. I owe the photograph (taken from life) to the kindness of Dr. Oraveiri, of Athens, a German physician, who has rendered service by a number of anthropological observations (for instance, in several cases of castrated

men) in Ceylon (at Belegama) in 1888. A young Singhalese in his twenty-fifth year was brought to me as a curious hermaphrodite, half-man and half-woman. His large breasts give plenty of milk; he was employed as "male nurse" to suckle a new-born infant whose mother had died at birth. The outline of his body was softer and more feminine than in the Greek shown in Fig. 104. As the Singhalese are small of stature and of graceful build, and as the men often resemble the women in clothing (upper part of the body naked, female dress on the lower



Fig. 104.—A Greek youth.

case). The gynecomastia in question is a Greek recruit in his twentieth year, who has both normally developed male organs and very pronounced female breasts. It is noteworthy that the other features of his structure are in accord with the other forms of the female sex. It reminds us of the marble statues of hermaphrodites which the ancient Greeks and Romans sculptors often produced. But one would only be a real hermaphrodite if he had ovaries internally besides the (externally visible) testicles.

I observed a very similar case during

part) and the dressing of the hair (with a comb), I first took the beardless youth to be a woman. The illusion was greater, as in this remarkable case gynecomastia was associated with cryptorchism—that is to say, the testicles had kept to their original place in the visceral cavity, and had not travelled in the normal way down into the scrotum. (Cf. Chapter XXIX.) Hence the latter was very small, soft, and empty. Moreover, one could feel nothing of the testicles in the inguinal canal. On the other hand, the male organ was very well, but unusually developed. It was

clear that this apparent hermaphroditism also was a real male.

Another case of practical gynaecomastia has been described by Alexander von Herboldt. In a South American forest he found a solitary settler whose wife had died in child-birth. The man had laid the new-born child on his own breast, in despair; and the continuous stimulation of the child's sucking movements had restored the activity of the mammary glands. It is possible that nervous suggestion had some share in it. Similar cases have been often observed in recent years, even among other male mammals (such as sheep and goats).

The great scientific interest of these facts is in their bearing on the question of heredity. The stem-history of the mammalium rests partly on its embryology (Chapter XXIV.) and partly on the facts of comparative anatomy and physio-

logy. As in the lower and higher mammals (the monotremes, and most of the marsupials) the whole lactiferous apparatus is only found in the female; and as these structures of it in the male only in a few younger marsupials, there can be no doubt that these important organs were originally found only in the female mammals, and that they were acquired by these through a special adaptation to needs of life.

Later, these female organs were transmitted to both sexes by heredity; and they have been maintained in all persons of either sex, although they are not physiologically active in males. This normal permanence of female lactiferous organs in both sexes of the higher mammals and men, is independent of any selection, and is a fine instance of the much-disputed "inheritance of acquired characters."

## CHAPTER XII.

### EMBRYONIC SHIELD AND GERMINATIVE AREA

The three higher classes of vertebrates which we call the amniotes—the mammals, birds, and reptiles—were notably distinguished by a number of peculiarities of their development from the five lower classes of the stem—the animals without an amnion (the anamnia). All the amniotes have a distinctive embryonic membrane known as the amnion (or "water-membrane"), and a special embryonic appendage—the allantois. They have, further, a large yolk-sac, which is filled with food-yolk in the reptiles and birds, and with a corresponding clear fluid in the mammals. In consequence of these later-acquired structures, the original features of the development of the amniotes are so much altered that it is very difficult to reduce them to the pre-genetic embryonic processes of the lower amnion-less vertebrates. The genetical theory shows us how to do this, by re-presenting the embryology of the lowest vertebrates, the skull-less amphioxus, on

the original form, and deducing from it, through a series of gradual modifications, the gastrulation and coelomation of the craniates.

It was somewhat fatal to the true acceptance of the chief embryonic processes of the vertebrates that all the older embryologists, from Malpighi (1678) and Wolff (1759) to Ober (1811) and Russak (1867), always started from the investigation of the bird's egg, and transferred to man and the other vertebrates the impressions they gathered from this. This classical object of embryological research is, as we have seen, a source of dangerous errors. The large round food-yolk of the bird's egg causes, in the first place, a flat aneurotic expansion of the small gastrula, and then to distract a development of this thin evaginated embryonic disk that the controversy as to its significance occupies a large part of embryological literature.

One of the most unfortunate errors that this led to was the idea of an original

antibiosis of germ and yolk. The latter was regarded as a foreign body, extrinsic to the real germ, whereas it is properly a part of it, an embryonic organ of nutrition. Many authors said there was no trace of the embryo until a later stage, and outside the yolk; sometimes the two-layered embryonic disk itself, at other times only the central portion of it (as distinguished from the germinative area, which we will describe presently), was taken to be the first portion of the embryo.

provinciate. This is clearly shown by the ova of the amphibia and cyclostomes, which explain the transition from the yolkless ova of the amphioxus to the large yolk-filled ova of the reptiles and birds.

It is precisely in the study of these difficult features that we see the invaluable value of phylogenetic considerations in explaining complex ontogenetic factors, and the need of separating macroscopic phenomena from paleoanatomical

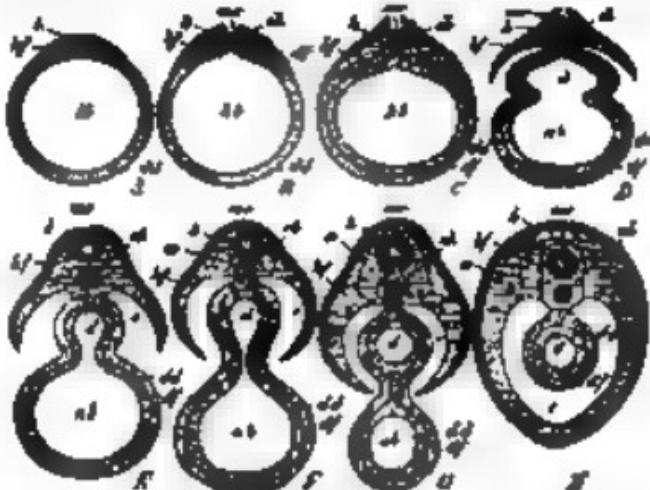


FIG. 10.—Stereogram of the dorsal marginal carinae from the right side, in transverse section (posterior). The ventral duct (A) has been cut out of the transverse carina (B); the duct (A) is the duct of the postero-lateral ducts and the right lateral duct; and underneath it lies the choana (C). The gular-laryngeal duct (D) has been indicated by the red colour (see Fig. 10a). The pharyngeal duct (E) is situated on the pharynx; the eye (F) lies at a distance from the mouth; no mandibular muscle buds (G) are visible. The larynx (H) is closed; the hyoid apparatus (I) is largely reduced. The pre-anal shield (J) begins to grow round the ventral duct (A) and the choana (C); the rectal duct (K) will form the ventral rectal duct. The epipharyngeal duct (L) has grown round the maxillary duct (M) and choana, the buccal cavity is closed, and the epipharyngeal duct (N) is situated in front of the maxillary duct (M).

In the light of the gastrula theory it is hardly necessary to dwell on the defects of this earlier view and the erroneous conclusions drawn from it. In reality, the first segmentation-ro-call, and even the stem-cell itself and all that issues therefrom, belong to the embryo. As the large original yolk-mass in the undivided egg of the bird only represents anucleated in the greatly enlarged ovum, so the later contents of its embryonic yolk-mass (whether yet segmented or not) are only a part of the cytoplasm which forms the

This is particularly clear as regards the comparative embryology of the vertebrates, because here the phylogenetic history of the stem has been already established by the well-known facts of paleontology and comparative anatomy. If this unity of the stem, on the basis of the similarities, were always borne in mind, we should not have these errors constantly occurring.

The many cases the congeneric relation of the embryo to the food-yolk has until now given one is a quite wrong idea of

the first and most important embryonic processes in the higher vertebrates, and has occasioned a number of false theories in connection with them. Thirty years ago the embryology of the higher vertebrates always started from the postulate that the first structure of the embryo is a flat, leaf-shaped disk; it was for this reason that the cell-layers that surround this germinal disk (also called *germative area*) are called "germinal layers." This flat germinal disk, which is round at first and then oval, and which is often described as the head or chorionite in the last bird's egg, is found at a certain part of the surface of the large globular *haemalysk*. I am convinced that it is nothing else than the closed, flattened gastrula of the birds. At the beginning of gastrulation the flat embryonic disk curves upwards, and separates on the lower side from the underlying large yolk-ball. In this way the flat layers are converted into tubes, their edges folding and joining together (Fig. 10g). As the embryo grows at the expense of the food-yolk, the tube becomes shorter and smaller, it is completely surrounded by the germinal layers. Later still, the remainder of the food-yolk only forms a small raised cap, the *proto-* or *archenteron* vesicle (Fig. 10j, m). This is enclosed by the yolk-layer, is connected by a thin stalk, the *yolk-sac*, with the central part of the gas-tube, and so finally, in most of the vertebrates, entirely absorbed by this (*H.*). The point at which this takes place, and where the gas-budly closes, is the *ventral nerve*. In the structures, in which the remainder of the yolk-cell remains trilobate and amphioxous, the yolk-sac, at length, penetrates the ventral wall. At birth the umbilical cord proceeds from here, and the point of closure remains throughout life in the side of the nail.

As the older embryology of the higher vertebrates was mainly based on the chick, and regarded the amphioxous embryo (or *formative-yolk*) and *food-yolk* (or *yolk-sac*) as original, it had also to look upon the flat leaf-shaped structure of the germinal disk as the primitive embryonic form, and asphyxiate the fact that hollow grooves were formed of these flat layers by folding, and closed later by the joining together of their edges.

This view, which dominated the whole treatment of the embryology of the higher vertebrates until thirty years ago, was

soundly false. The gastral theory, which has its chief application here, teaches us that it is the very reverse of the truth. The cup-shaped gastrula, in the body-wall of which the two primary germlined layers appear from the first as closed tubes, is the original embryonic form of all the vertebrates, and all the multicellular invertebrates; and the flat germlined disk with its superficially expanded germlined layers is a later, secondary form, due to the neogenetic formation of the large food-yolk, and the gradual removal of the gas-layers over its surface. Hence the actual folding of the germlined layers and their conversion into tubes is not an original and primary, but a much later and temporary, evolutionary process. In the phylogeny of the vertebrate embryonic groups we may distinguish the following three stages:—

A First Stage Primary germlined layers	B Second Stage Secondary germlined layers	C Third Stage Secondary germlined layers
The <i>cup-shaped</i> gastrula, with the two primary germlined layers in the body-wall of the food-yolk, and the gas-tube surrounded by the germinal layers.	The <i>cup-shaped</i> gastrula, with the two primary germlined layers in the body-wall of the food-yolk, and the gas-tube surrounded by the germinal layers.	The <i>flat</i> (or <i>leaf</i> -shaped) gastrula, with the two primary germlined layers in the body-wall of the food-yolk, and the gas-tube surrounded by the germinal layers.

As this theory, a logical conclusion from the gastral theory, has been fully substantiated by the comparative study of gastrulation in the best few groups, we must exactly reverse the hitherto prevalent views of trituration. The yolk-cell is not to be treated, as was done formerly, as if it were originally amphioxous in the embryo, but as an essential part of it, a part of its *original type*. The primitive part of the gastrula lies, on this view, *first* divided into two parts in the higher invertebrates as a result of the neogenetic formation of the food-yolk—the permanent gut (*metagenesis*), or permanent *amphioxous canal*, and the yolk-cell (*division*), or *amphioxous vesicle*. This is very clearly shown by the comparative embryology of the fishes and amphioxus. In these cases the whole yolk undergoes cleavage of first, and forms a yolk-groove, composed of yolk-cells, in the ventral wall

of the primitive gut. But it afterwards becomes so large that a part of the yolk does not divide, and is used up in the yolk-sac that is cut off outside.

When we make a comparative study of the embryology of the amphibia, like the frog, the chick, and the rabbit, there cannot, in my opinion, be any further doubt as to the truth of this position, which I have held for thirty years. Hence in the light of the gastrula theory we must regard the features of the amphibia as the only and real primitive structure among all the vertebrates, departing very little from the palingenic embryonic form. In the cyclostomes and the frog these features are, on the whole, not much altered congenitally, but

the older, oviparous mammals, the monotremes, behave in the same way as the reptiles and birds. But the corresponding embryonic processes in the viviparous mammals, the marsupials and placentals, are very elaborate and distinctive. They were formerly quite misinterpreted; it was not until the publication of the studies of Edward van Hogenben (1875) and the later research of Schaeffer, Kupffer, Ebel, and others, that light was thrown on them, and we were in a position to bring them into line with the principles of the gastrula theory and trace them to the archaic forms of the lower vertebrates. Although there is no independent food-yolk, apart from the functioning yolk, in the mammal ovum, and although its segmentation is total and batocerous, nevertheless a large yolk-sac is formed in their embryos, and the "embryo proper" spreads leaf-like over its surface, as in the reptiles and birds, which have a large food-yolk and partial segmentation. In the marsupials, as well as in the latter, the flat, leaf-shaped gerarial disk separates from the yolk-sac, and its edges join together and form tubes.

How can we explain this curious anomaly? Only as a result of very characteristic and peculiar ontogenetic modifications of the embryonic process, the real nature of which must be sought in the change in the rearing of the young on the part of the viviparous mammals. These are clearly connected with the fact that the ancestors of the viviparous mammals were oviparous animals like the present monotremes, and only gradually became viviparous. This can no longer be questioned now that it has been shown (1884) that the monotremes, the lowest and oldest of the mammals, still lay eggs, and that these develop like the ova of the reptiles and birds. Their nearest descendants, the marsupials, formed the habit of retaining the eggs, and enveloping them in the



FIG. 101.



FIG. 102.

FIG. 101.—The second cleavage results in the formation of a solid plate (blastoderm) of various thicknesses of older yolk, a cavity remaining in the center of which forms the future body of the embryo; a group of dark cells representing the neural layer or neurula.

FIG. 102.—The same as before, showing a more advanced stage of the embryo.

they are very much so in the chick, and most of all in the rabbit. In the hind-gut of the amphibia and in the fore-gut of the lamprey and the frog the germinal layers are found to be closed tubes or vesicles from the first. On the other hand, the chick-embryo (in the new laid, but not yet hatched, egg) is a flat circular disk, and it was not easy to recognise this as a real gastrula. Rucker and Goetz have, however, achieved this. As the discoid gastrula grows round the large globular yolk, and the permanent gut then separates from the outlying yolk-sac, we find all the processes which we have shown (diagrammatically) in Fig. 103—processes that were hitherto regarded as principal ones, whatever they are mainly secondary.

ovule; the latter was thus converted into a womb (*uterus*). A nutritive fluid that was secreted from its wall, and passed through the wall of the Mucula, now served to feed the embryo, and with the place of the food-yolk. In this way the original food-yolk of the *mesoblast* gradually atrophied, and at last disappeared so completely that the partial *proto-angulation* of their descendants, the rest of the *mesoblasts*, once more became total. From the descendants of the former was evolved the distinctive appendages of the latter.

It is only by this phylogenetic explanation that we can understand the formation and development of the placenta, and hitherto totally misunderstood, Mucula of the mammal. The vesicular condition of the mammal embryo was discovered two years ago (1957) by Wagner de Groot. He found in the uterus of a rabbit four days after insemination small, round, loose, transparent vesicles, with a double envelope. However, Groot's discovery passed without recognition. It was not until 1957 that these vesicles were rediscovered by Gloor, and they were closely studied in 1958 by Blitsch in the rabbit (Figs. 106, 107). They are found in the womb of the rabbit, the dog, and other small mammals, a few days after copulation. The fixtures out of the mucula, when they have left the ovary, are fertilized either here or in the oviduct immediately afterwards by the invading spermatoma. (As to the womb and oviduct, see Chapter XXIX.) The cleavage and formation of the gastrula take place in the oviduct. Either here in the oviduct or after the mammal gastrula has passed into the uterus it is converted into the globular vesicle which is shown externally (Fig. 106), and in section in Fig. 107. The thick, outer, structureless envelope that encloses it is the original *ovule* or *zona pellucida*, modified, and clothed with a layer of albumen that has been deposited on the outside. From this stage the envelope is called the *external membrane*, the *perivitelline sac* or *proctochorion* (*a*). The real wall of the vesicle

enclosed by it consists of a single layer of *ectodermic cells* (*b*), which are flattened by mutual pressure, and generally hemispherical; a light nucleus shines through their fine-grained protoplasm (Fig. 107). At one part (*c*) inside this hollow ball we find a circular disc, formed of darker, taller, and rounded cells, the dark-grained *endodermic cells* (Fig. 108).

The characteristic embryonic form that the developing mammal now exhibits up to the present usually been called the "Mucula" (Blitsch), "macrodian embryo" (Boas), "vesicular embryo" (Saville), "blastoderm," or, briefly, "blastosphere". The wall of the hollow vesicle, which consists of a single layer of cells, was called the "blastoderm," and was supposed to be equivalent to the cell-layer of the same name that forms the wall of the real blastula of the amphioxus and

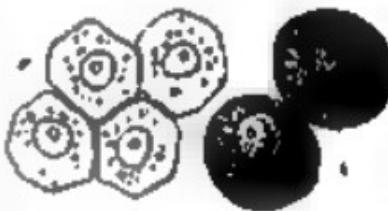


FIG. 106.

FIG. 107.

FIG. 106.—Some endodermic cells from the anterior region of the embryo.

FIG. 107.—Two ectodermic cells from the anterior region of the embryo.

many of the vertebrates (such as *Moschetta*, Fig. 29 *N*, *O*). Formerly this real Mucula was generally believed to be equivalent to the embryonic vesicle of the mammal. What is called the "blastula" of the mammal and the real blastula of the amphioxus and many of the invertebrates are totally different embryonic structures. The latter (blastula) is palliative, and precedes the formation of the gastrula. The former (blastodermic vesicle) is neogenetic, and follows gastrulation. The globular wall of the blastula is a real Mucula, and consists of homogeneous (blastodermic) cells; it is not yet differentiated into the two primary germinal layers. But the globular wall of the mammal vesicle is the differentiated ectoderm, and at one point in it we find a circular disk of quite different cells—the endoderm. The round

\* In this and the other mammals the fertilization of the egg probably takes place in a tube, in the neighborhood of the *oviduct*, which comes from the floor of the *uterus* to the top of the *ovary*. After the whole process of the ordinary ovulation the whole apparatus of the oviduct, which passes into the womb, is closed, and from this time the several layers of the oviduct are rapidly taken away in the course of the

cavity, filled with fluid, inside the red blastula is the segmentation-cavity. But the smaller cavity within the ~~surrounding~~ secondary vehicle is the yolk-sac cavity, which is

which we have considered previously (Chapter XII). For these reasons it is very necessary to recognise the secondary ~~secondary~~ vehicle in the expanded (*gastrula*)



Fig. 116.



Fig. 117.

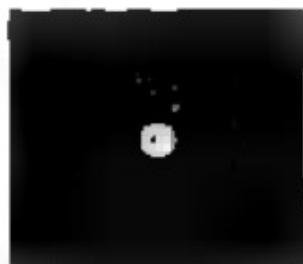


Fig. 118.



Fig. 119.



Fig. 120.

connected with the subjacent gas-cavity. This primitive gas-cavity passes directly into the segmentation-cavity in the amermale. In consequence of the particular ontogenetic changes in their gastrulation,

Figs. 116-119.—*Yolk-sac* of a *rotifile* from the uterus, one month old at dissection. The segmentation-cavity (d) has expanded a little. From the beneath it surrounds (c) the yolk-sac cavity (a), the mouth of which (b) is situated near the anterior end of a slightly longitudinal depression (Fig. 116-118, from *Huxley*).

Fig. 120.—The same *yolk-sac*, seen in profile. Letter same as Fig. 116.

Fig. 121.—*Yolk-sac* of a *rotifile* from the uterus, one month old at dissection. The blastoderm is clearly seen for the most part throughout (d). The embryo, of outer profile, is below (a).

Fig. 122.—The same *yolk-sac*, seen in profile. Letter same as Fig. 121.

Fig. 123.—*Yolk-sac* of a *rotifile* from the uterus, one month old at dissection. The embryonic vessels (c) pass obliquely throughout (d), only crossing superficially (b).

(*gasula* or *blastocysta*) is a characteristic structure peculiar to this class, and distinguishes it carefully from the primary division of the amphioxus and the invertebrates.

The small, circular, whitish, oval spot which the germinative disk (Fig. 106) forms at a certain part of the surface of the clear and transparent embryonic vesicle has long been known to science,



FIG. 112.—*Dorsal germinative area* of the *polyp*, divided into several light and some dark sectors; the peripheral dark zone (arrow) gives the light area more color so that it is the dark ground appearing through it.

and denoted by the germinative disk of the birds and reptiles. Sometimes it has been called the germinative spot, and usually the germinative area. From the area the further development of the embryo proceeds. However, the larger part of the embryonic vesicle of the mammal is not directly used for building up the later body, but for the construction of the ectoplacental umbilical vesicle. The embryo separates from this in proportion as it grows at its expense; the two are often connected by the peduncle (the stalk of the yolk-sack), and thus maintains the direct communication between the cavity of the umbilical vesicle and the forming visceral cavity (Fig. 103).

The germinative area or germinative disk of the mammal consists at first (like the germinative disk of birds and reptiles) merely of the two primary germinative layers, the ectoderm and endoderm. But soon there appears in the middle of the circular disk between the two a third stratum of cells, the rudiment of the middle layer or Mesogerm layer (*mesoderm*). This middle germinative layer consists from the first, as we have seen in the tenth Chapter, of two separate epithelial plates, the two layers of the colom-pouches (parietal and viseral). However, in all the amniotes (in account of the large formation of yolk) these thin middle plates are so firmly pressed together that they seem to represent a

single layer. It is thus peculiar to the mammals that the middle of the germinative area is composed of four germinative layers, the two limiting (or primary) layers and the middle layers between them (Figs. 96, 97). These four secondary germinative layers can be clearly distinguished as soon as what is called the solid-gastric (or "embryonic sickle") is formed at the border of the germinative area. At the borders, however, the germinative area of the mammal only consists of two layers. The rest of the wall of the embryonic vesicle consists at first (but only for a short time in most of the mammals) of a single layer, the outer germinative layer.

From this stage, however, the whole wall of the embryonic vesicle becomes two-layered. The middle of the germinative area is much thickened by the growth of the cells of the middle layers, and the latter lie at depths at the same time, and increase at the border of the disk all around. Lying close on the outer layer throughout, it grows over its inner surfaces at all points, covers first the upper and then the lower hemisphere, and at last closes in the mouth of the inner layer (Figs. 106-111). The wall of the embryonic vesicle now consists throughout of two layers of cells, the ectoderm without and the endoderm within. It is only in the centre of the circular area, which,



FIG. 113.—*Dark area*, with the opaque white border of the dark area visible.

becomes thicker and thicker through the growth of the middle layers, that it is made up of all four layers. At the same time, small structureless tufts or warts are deposited on the surface of the outer

ovulema or prechorion, which has been raised above the embryonic vesicle (Figs. 122-124 a).

We may now disregard both the outer ovulema and the greater part of the

layered to the four-layered stage, the two-layered mesoderm developing from the median primitive groove between the endoderm and ectoderm (Figs. 2a-2g).

The first change in the round gerinal disk of the chick is that the cells at its edges multiply more briskly, and form darker nuclei in their protoplasm. This gives rise to a dark ring, more or less sharply set off from the lighter center of the gerinal disk (Fig. 115). From this point the latter takes the name of the "light area" (*area pallens*), and the darker ring is called the "dark area" (*area nigra*). In a strong light, as in Figs. 115-117, the light area seems darker because the dark ground is seen through it; and the dark area seems whiter. The circular shape of the area now changes into elliptic, and then immediately into oval (Figs. 116, 117). One end seems to be broader and blunter, the other narrower and more pointed, the former corresponds to the anterior and the latter to the posterior section of the subsequently body. At the same time, we can already trace the characteristic bilateral form of the body, the distinction of right and left, before and

FIG. 115.—First multiplied edge of the 1000-  
micron diameter chick in form. As the development progresses, this edge becomes more and more like a dark ring, and the center can first consist of the light area. The oval shape of the  
area also becomes evident, and so does the  
median primitive groove. (From Sharpe.)

vesicle, and occupies our attention on the germinative area and the four-layered embryonic disk. It is here alone that we find the important changes which lead to the differentiation of the first organs. It is immaterial whether we examine the germinative area of the mammal (the rabbit, for instance) or the gerinal disk of a bird or a reptile (such as a lizard or tortoise). The embryonic processes we are now going to consider are essentially the same in all members of the three higher classes of vertebrates which we call the amniotes. Man is found to agree in this respect with the rabbit, dog, etc.; and in all these mammals the germinative area undergoes essentially the same changes as in the birds and reptiles. They are most frequently and accurately studied in the chick, because we can have incubated hens' eggs at any quantity at any stage of development. Moreover, the round gerinal disk of the chick passes immediately after the beginning of incubation (within a few hours) from the two-



FIG. 115.—First multiplied gerinal edge of the 1000-micron diameter chick, showing the dark area (germinative area). (From Sharpe.)

layers. This will be made clearer by the "primitive streak," which appears at the posterior end.

At an early stage an opaque spot is seen in the middle of the close germinative

area, and this also passes from a circular to an oval shape. At first this shield-shaped marking is very delicate and barely perceptible; but it soon becomes clearer, and now stands out as an oval shield, surrounded by two rings or areas (Fig. 117). The inner and brighter ring is the remainder of the pallid area, and the dark outer ring the remainder of the opaque area; the opaque shield-like spot itself is the first rudiment of the dorsal part of the embryo. We give it briefly

"post." and "germinative area," are used in many different sense—and this has led to much confusion in embryonic literature—we must explain very clearly the real significance of these important embryonic parts of the amniote. It will be useful to do so in a series of formal principles:—

1. The so-called "first trace of the embryo" in the amniote, or the embryonic shield, in the centre of the pallid area, consists merely of an early differen-

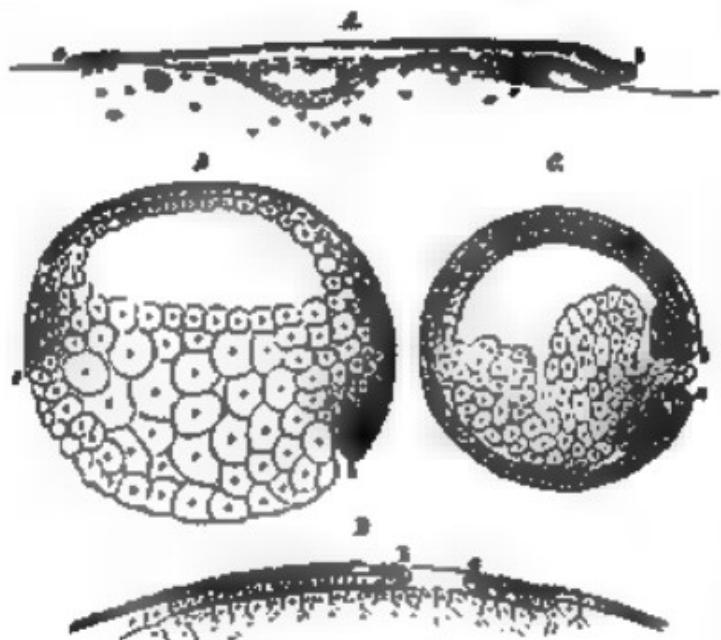


FIG. 118.—Vertical longitudinal section of the posterior of the vertebrate. (Post. Axis). A, dissepiment of a shark (*Ptychostomus*); B, dissepiment of a conger (*Conger*). C, emplastrum of an amphiuma? (*Ptych.*); D, emplastrum of an ammodyte (*Ammodytes*); E, ventral, & dorsal, & of the posterior mouth.

the name of embryonic shield or dorsal shield. In most works this embryonic shield is described as "the first rudiment of the embryo," or "principle embryo." But this is wrong, though it rests on the authority of Baer and Haeckel. As a matter of fact, we already have the embryo in the stem-cell, the gastrula, and all the subsequent stages. The embryonic shield is simply the first rudiment of the dorsal part, which is the *second* rudiment. As the older sense of "embryonic shield"

isation and formation of the middle dorsal parts.

2. Hence the best name for it is "the dorsal shield," as I proposed long ago.

3. The germinative area, in which the first embryonal blood-vessels appear at an early stage, is not opposed as an external area to the "embryo proper," but is a part of it.

4. In the same way, the yolk-sac or the umbilical vesicle is not a foreign external

appendage of the embryo, but an evolving part of its primitive gut.

5. The dorsal shield gradually separates from the germulative area and the yolk-sac, its edges growing dorswards, and folding together to form ventral plates.

6. The yolk-sac and vesicle of the germulative area, which soon spread over the whole surface, are, therefore, real embryonic organs, or homologous parts of the embryo, and have a transitory importance in connection with the nutrition of the growing later body; the latter may be called the "parthenial body" in contrast to them.

The relation of these eogenetic features of the amniote to the phylogenetic structure of the older metazoic vertebrates may be expected in the following terms: The original gastrula, which completely包圍着 the embryo, like that in the annelids, cyclostomes, and amphibia, is early divided into two parts in the annelids—the endoderm shield, which represents the dorsal outline of the permanent body, and the temporary embryonic organs of the germulative area and its homologues, which soon grow over the whole of the yolk-sac. The differences which are due to the various classes of the vertebrates seem to these important particular can only be fully understood when we bear in mind their phylogenetic relations on the one hand, and, on the other, the phylogenetic modifications of structures that have been brought about by changes in the rearing of the young and the variation of the food-yolk.

We have already described in the ninth chapter the changes which this increase and decrease of the nutritive yolk cause in the form of the gastrula, and especially in the situation and shape of the primitive mouth. The primitive mouth or proboscis is originally a simple round aperture at the lower pole of the long axis, its dorsal lip is above and ventral lip below. In the amphibia this primitive mouth is a little exterior, or shifted to the dorsal side (Fig. 32). The aperture increases with the growth of the food-yolk to the cyclostomes and ganoids; in the sturgeons it lies almost on the equator of the round ovum,

the ventral lip ( $\delta$ ) is front and the dorsal lip ( $\delta\delta$ ) behind (Fig. 119 A). In the wide-mouthed, circular discoid gastrula of the elasmobranch or primitive fishes, which spreads quite flat on the large food-yolk, the anterior semi-circle of the border of the disk is the ventral, and the posterior semi-circle the dorsal lip (Fig. 119 A). The amphioxian amphiblasts are directly connected with their earlier lithostrophula, the diploblasts and gonoids, and further the older actinians (*Coelenterata*); they have retained their total unequal segmentation, and their small primitive mouth (Fig. 119 C,  $\delta\delta$ ), blocked up by the yolk-stopper-line at the limit of the dorsal and ventral surface of the embryo (at the lower pole of its equatorial axis), and there again has an upper dorsal and a lower ventral lip ( $\delta$ ,  $\delta\delta$ ). The formation of a large food-yolk followed again in the development of the annelids, the peribranchia of protostomia, derived from the amphibia (Fig. 119 D). But here the segmentation of the body-shield was placed only in the ventral wall of the peribranchia, so that the dorsal proboscis mouth lying behind was forced upwards, and came to lie on the back of the dorsal "epibranchia"; thus (in contrast to the case of the velum, Fig. 119 A) the dorsal lip ( $\delta$ ) had to be front, and the ventral lip ( $\delta\delta$ ) behind (Fig. 119 D). This feature was transmitted to all the annelids, whether they retained the large food-yolk (nudibranchs, and monopeltids), or lost it by emptying (the oligochaetes mammals).

This phylogenetic explanation of gastrulation and differentiation, and the comparative study of them in the various vertebrates, throw a clear and full light on every ontogenetic phenomena, on to which the most obscure and confused opinions were prevalent thirty years ago. In this we see especially the high scientific value of the biogenetic law and the careful separation of ontogenetic from phylogenetic processes. To the opponents of this law the real explanation of these remarkable phenomena is impossible. Hence, and in every other part of embryology, the true key to the solution lies in phylogeny.

## CHAPTER XIII.

## DORSAL BODY AND VENTRAL BODY

The earliest stages of the human embryo are, for the reasons already given, either quite unknown or only imperfectly known to us. But as the subsequent embryonic forms in man behave and develop just as they do in all the other mammals, there cannot be the slightest doubt that the preceding stages also are similar. We have been able to see in, the egg-mass of the human embryo (Fig. 95), by successive sections through its primitive mouth, that its two ectomorphae are developed in just the same way as in the

It is in the middle line of this that the primitive streak appears (Fig. 322 *ph*). The narrow longitudinal groove in it—the so-called "primitive groove"—is, as we have seen, the primitive mouth of the gastrula. In the gastrula-embryos of the mammals, which are much modified anatomically, this slant-shaped depression is lengthened so much that it soon encircles the whole of the hinder half of the dorsal shield; as we find in a rabbit-embryo of six to eight days (Fig. 322 *pr*). The two swollen parallel borders that



FIG. 123.—Rabbit-embryo section of a seven-day-old rabbit with oral endodermis intact, and a few free streaks of tissue on each side. (Photo, W. H. Johnson.) As shown above, the mouth is at the upper limit of the mouth, a result of the two junctional epithelial layers, the lower one being that from the outer layer.

rabbit (Fig. 95); moreover, the peculiar course of the gastrulation is just the same.

The germinative area forms in the human embryo in the same way as in the other mammals, and in the middle part of this we have the embryonic shield, the purpose of which we considered in the previous chapter. The next changes in the embryonic disk, or the "embryonic spot," take place in corresponding fashion. These are the changes we are now going to consider more closely.

The chief part of the web embryonic shield is at first the narrow hinder end;



and this median furrow are the side lips of the primitive mouth, right and left. In this way the bilateral-symmetrical type of the vertebrate becomes pronounced. The subsequent head of the embryo is developed from the broader and rounder fore-half of the dorsal shield.

In this fore-half of the dorsal shield a median furrow quickly makes its appearance (Fig. 123 *pf*). This is the broader dorsal furrow or mid-dorsal groove, the first beginning of the central nervous system. The two parallel dorsal or mid-dorsal swellings that enclose it grow

together over it; afterwards, and before the medullary tube. As is seen in transverse sections, it is formed only of the outer germinal layer (Figs. 26, 159). The floor of the primitive mouth, however, is, in

one place, at the important point where the outer layer bends over the inner, and from which the two caecae pouches grow between the primary germinal layers. Thus the median primitive furrow (*pr*)

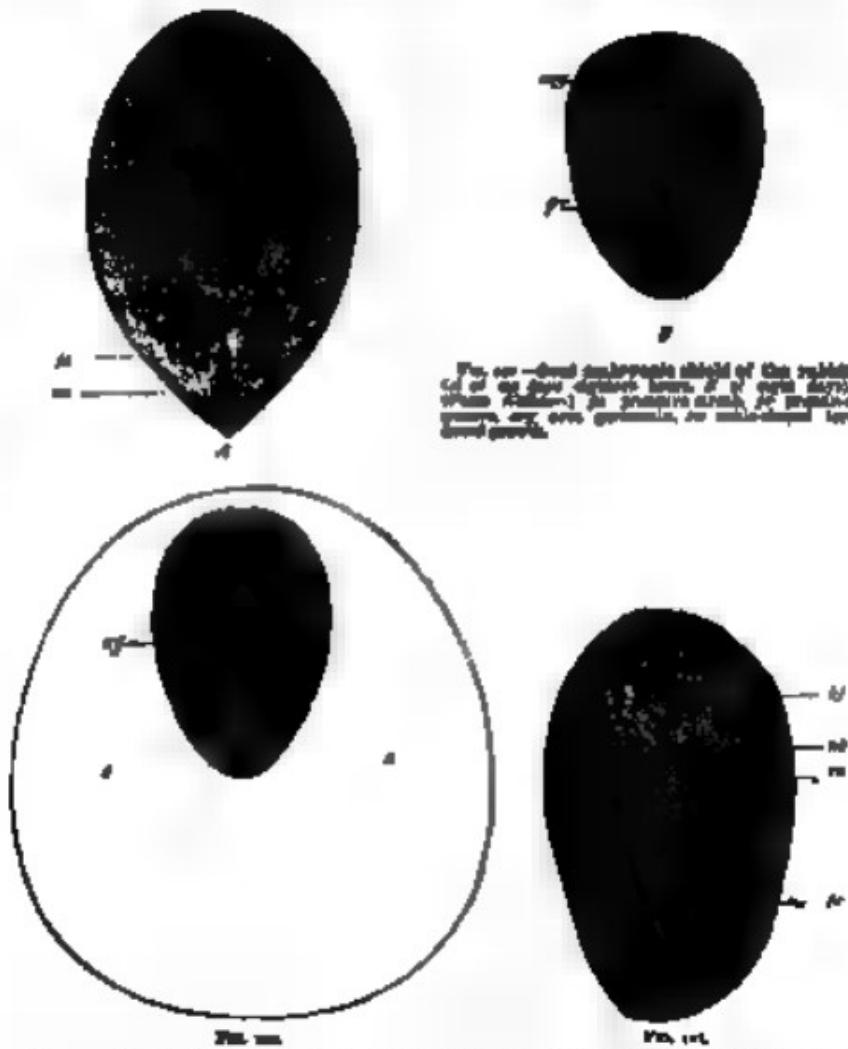


FIG. 14.—Dorsal shield (*d*), mid-venter-shield area (*m*), and anterior-shield area (*a*) of a rabbit-embryo of eight days. (From Amstutz.) *v*, ventral shield.

FIG. 15.—Dorsal shield (*d*) and anterior-shield area (*a*) of a rabbit-embryo of eight days. (From Amstutz.) *v*, ventral shield; *m*, mid-venter-shield area; *d*, dorsal shield; *a*, anterior shield.

in the hind-half and the postero-mediary furrow (*ef*) in the fore-half of the oral shield are totally different structures, although the latter seems to a superficial observer to be merely the forward continuation of the former. Hence they



FIG. 106.—Longitudinal section of the nervous system of amphipods (from de Witz). *d*, anterior of primitive gut; *f*, postero-mediary furrow; *m*, nerve-canal; *n*, nerve-centre; *v*, the ventral segment; *v*, nerve-process. (One millim.)

were formerly always confused. The error was the more pardonable as immediately afterwards the two grooves do actually pass into each other in a very remarkable way. The point of transition is the remarkable *anastomotic canal* (Fig. 106 *cn*). But the direct connection which is thus established does not last long, the two are soon definitely separated by a partition.

The enigmatic *anastomotic canal* is a very old embryonic organ, and of great phylogenetic interest, because it arises in the same way in all the chordotonia (both tunicates and vertebrates). In every case it touches or embraces like an arch the posterior end of the *chorda*, which has been developed here in front out of the middle line of the primitive gut (between the two median-folds of the notula groove) ("head-process," Fig. 103 *A*). These very ancient and strictly hereditary structures, which have no physiological significance to-day, deserve (as "relictive organs") our closest attention. The tenacity with which the useless anastomotic canal has been transmitted down to man through the whole series of vertebrates is of equal interest for the theory of descent in general, and the phylogeny of the chordotonia in particular.

The connection which the anastomotic canal (Fig. 106 *cn*) establishes between the dorsal nerve-tube (*dn*) and the ventral gut-tube (*vt*) is seen very

plainly in the amphipods in a longitudinal section of the notula, as soon as the primitive mouth is completely closed at its hinder end. The medullary tube has still at this stage an opening at the forward end, the *neurocrus* (Fig. 83 *af*). This opening also is afterwards closed. There are then two completely closed canals over each side—the medullary tube above and the gastric tube below, the two being separated by the *chorda*. The same features as in the ascidians are exhibited by the related tunicates, the salidiids.

Again, we find the neuromeric canal in just the same form and situation in the amphipods. A longitudinal section of a young amphipod (Fig. 106 *ad*) shows how we may perceive first the still open primitive mouth (*pm*) either into the wide primitive gut-cavity (*pg*) or the narrow underlying nerve-tube. A little later, when the primitive mouth is closed, the narrow neuromeric canal (Fig. 106 *ac*) represents the arched connection between the dorsal medullary canal (*mc*) and the ventral gastric canal.

In the annelids this original curved form of the neuromeric canal cannot be found at first, because here the primitive mouth crevices completely over to the

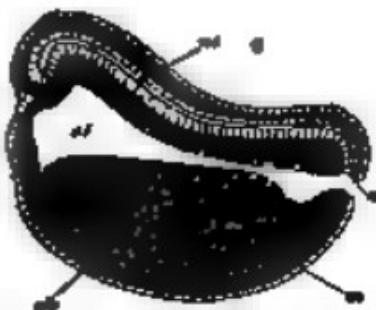


FIG. 107.—Longitudinal section of the amphipods at a later stage (from de Witz). *dn*, nerve-centre; *f*, dorsal nerve-tube; *m*, nerve-canal; *vt*, ventral gut-tube.

dorsal surface of the gut-tube, and is converted into the longitudinal furrow we call the primitive groove. Hence the primitive groove (Fig. 107 *fg*), examined above, appears to be the straight

continuation of the fore-tube and younger oesophagus (Fig. 116). The divergent hind legs of the latter audience the anterior end of the fore-tube. Afterwards we have the complete closure of the primitive mouth, the dorsal mouth-

while these important processes are taking place in the axial part of the dorsal shield, its external form also is changing. The oval form (Fig. 117) becomes like the sole of a shoe or sandal, tyro-shaped or finger-boot-shaped (Fig. 118). The middle third does not grow in width as quickly as the posterior, and still less than the anterior third; thus the shape of the germinative body becomes somewhat narrow at the waist. At the same time, the oval form of the germinative area returns to a circular shape, and the upper palaeid area separates more clearly from the epigynous anterior area (Fig. 119). The completion of the circle in the area marks the limit of the formation of muscle-groups in the mesoderm.

The characteristic sandal-shape of the dorsal shield, which is



FIG. 116. Longitudinal section of a trilobite. (From Hinde.) — ab, ad, ar, av, co, ex, gl, ha, me, mgl, mgl', mgl'', mgl''', mgl'''', mgl'''''.

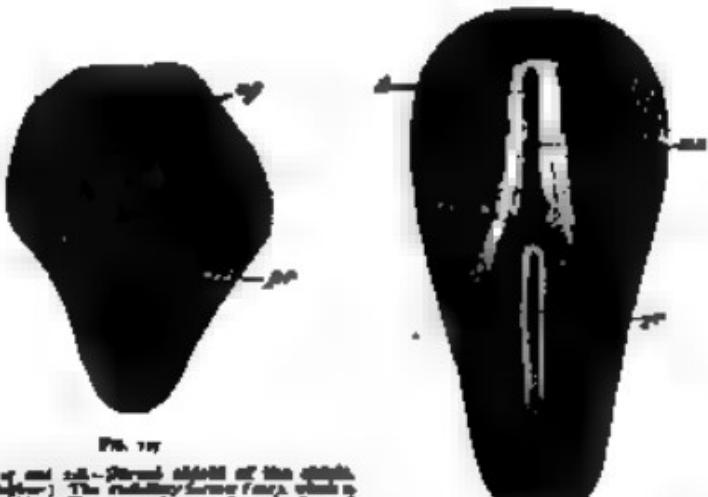


FIG. 117.

FIG. 117 and 118.—Dorsal shield of the shield. Other figures: 1. The medullary tube (Fig. 119), which is the 2d cavity in Fig. 120—compare with the hinder end of the fore and of the posterior groove (Fig. 120). FIG. 118.

FIG. 118.

joining to form the medullary tube and growing over it. The germinative canal then leads directly, in the shape of a narrow arch-shaped tube (Fig. 120 a), from the medullary tube (Fig. 119) to the gastric tube (Fig. 120). Directly in front of it is the latter end of the chela (Fig.

determined by the narrowness of the middle part, and which is compared to a violin, tyre, or shoe-sole, persists for a long time in all the annelids. All mammals, birds, and reptiles have substantially the same construction at this stage, and even for a longer or shorter

period after the division of the primitive segments into the epiblast-shield has begun (Fig. 232). The human embryonic shield guarantees the mesoblast-form in the second week of development; whereas

the rabbit and Fig. 235 in the opossum, as does each other that we can either not distinguish them at all or only by means of quite subordinate peculiarities in the size of the various parts. Moreover, the human sandal-shaped embryo cannot at this stage be distinguished from those of other mammals, and it particularly resembles that of the rabbit. On the other hand, the embryonic form of these flat sandal-shaped embryos is very different from the corresponding forms of the lower animals, especially the amniotes (amphibians). Nevertheless, the body is just the same in the essential features of its structure as that we find in the chordates of the latter (Figs. 236-238), and in the embryonic forms which immediately develop from it. The striking material difference is here again



FIG. 232.—Longitudinal section of the bladder and of a digit of a rabbit's embryo at the beginning of the second week, the dorsal part being the epiblast-shield and the ventral part being the hypoblast-shield. The amniotic fluid (al.) separates the epiblast-shield from the hypoblast-shield. In the center of the epiblast-shield is a small cavity (m.). A portion of the epiblast-shield is shown in a transverse section in the inset.

the end of the week our wide-shaped amniote has a length of about one-twelfth of an inch (Fig. 233).

The complete bilateral symmetry of the vertebrate body is very early indicated in the oval form of the amniotic shield (Fig. 237) by the median primitive vesicle. In the mandibular form it is two rows pronounced (Figs. 231-235). In the buccal part of the amniotic shield a darker central and a lighter peripheral zone become more obvious; the former is called the *metaplaea* (Figs. 234-235), and the latter the *pariplaean zone* (p. 6); from the first we get the dorsal and from the second the ventral half of the body-wall. The striae-zone of the amniotic ectoderm would be called more appropriately the *dorsal zone* or *dorsal shield*, since it develops the whole of the dorsal half of the later body (or permanent body)—that is to say, the dorsal body *proper*. Again, it would be better to call the "pariplaean zone" the *ventral zone* or *ventral shield*; from it develop the ventral "lateral plates," which afterwards separate from the amniotic vesicle and form the ventral body (*hypoplasia*)—that is to say, the ventral half of the permanent body, together with the body-cavity and the gastric canal that it encloses.

The sole-shaped gut-tube-shield of all the amniotes are still, at the stage of construction which Fig. 235 illustrates in

due to the fact that in the pell-mell condition of the amniotes (Figs. 23, 24) and the arthropods (Figs. 25, 26) the ga-



FIG. 233.—Carpined view of a generalized disk of the rabbit, with well-defined epiblast-shield surrounding about the ventral. The deep circular fold (c.) is the epiblast area. The pointed arm (e.) is a hypoblast fold, like the amniotic shield itself (A.). In the center is the dorsal nerve or medullary furrow (d.).

well and body-wall form closed tubes from the first, whereas in the eogenetic embryos of the amniotes they are forced to expand leaf-wise on the surface owing to the great extension of the food-yolk.

It is all the more notable that the early separation of dorsal and ventral halves takes place in the same rigidly hereditary fashion in all the vertebrates. In both the ascidians and the cyclostomes the dorsal body is about this period separated from the ventral body. In the middle part of the body this division has already taken place by the construction of the channel between the dorsal nerve-tube and the ventral canal. But in the outer or lateral

portion step by step with interesting changes in the notochord, while the entoderm changes little at first. We can study these processes best in transverse sections, made vertically to the surface through the sole-shaped embryonic shield. Such a transverse section of a chick-embryo, at the end of the first day of incubation, shows the gut-gland layer as a very simple epithelium, which is spread like a leaf over the outer surface of the

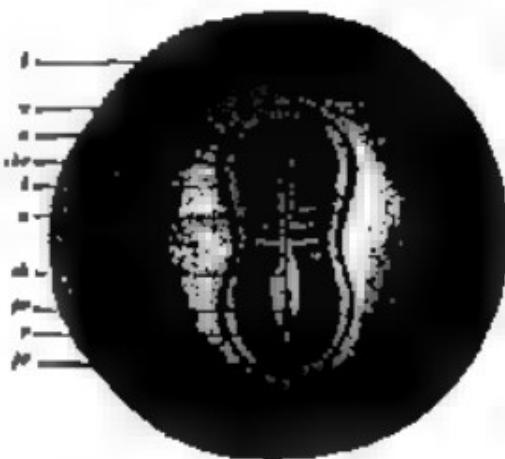


FIG. 129.



FIG. 130.

Fig. 129.—Diagram of the embryo, showing the moment of its birth or division. (From Winkler.) It is the greatest diameter within the normal incubation time. A line of the ventral plate, *d*, dorsal shield, *v*, the fore part, or the first primary segment, *n*, neck, *b*, the forepart, or primary groove (or mouth).

Fig. 130.—Standard-sized embryo, showing at a moment of slight change, with the fore part of the forepart seen (as appears at present view). (From Winkler.) *d*, dorsal (dorsal); *v*, ventral (ventral) shield. In the narrow middle part the three primary segments may be seen.

part of the body it is only brought about by the division of the outer portions into five sections—a dorsal ghemeric (dorsal segment or provertebra) and a ventral ghemeric (or ventral segment)—by a frontal constriction. In the mesoblast each of the former yields a nosophore pouch, and each of the latter a nosophore or gonad.

These important processes of differentiation in the mesoblast, which we will consider more closely in the next chapter,

are well shown (Fig. 131). The shield (*sh*) has separated from the dorsal middle line of the notochord; to the right and left of it are the two halves of the notochord, or the two otono-folds. A narrow cleft in the latter indicates the body-cavity fold (*bcf*); this separates the two planes of the otono-pouches, the lower (visceral) and upper (parietal). The broad dorsal furrow (*df*) formed by the notochordal plate (*np*) is still wide open, but is divided from the lateral body-plate

(A) by the parallel medullary swellings, which eventually close.

During these processes important changes are taking place in the outer germinal layer (the "skin-sense layer"). The continued rise and growth of the dorsal swellings cause their higher parts to bend together at their free borders, approach nearer and nearer (Fig. 136 A), and finally unite. Thus in the end we

discover it is a thoroughly natural process. The physiognomic explanation of it is that the central nervous system is the organ by means of which all intercourse with the outer world, all psychic action and sense-perception, are accomplished; hence it was found to develop originally from the outer and upper surface of the body, or from the outer skin. The medullary folds afterwards separate completely from

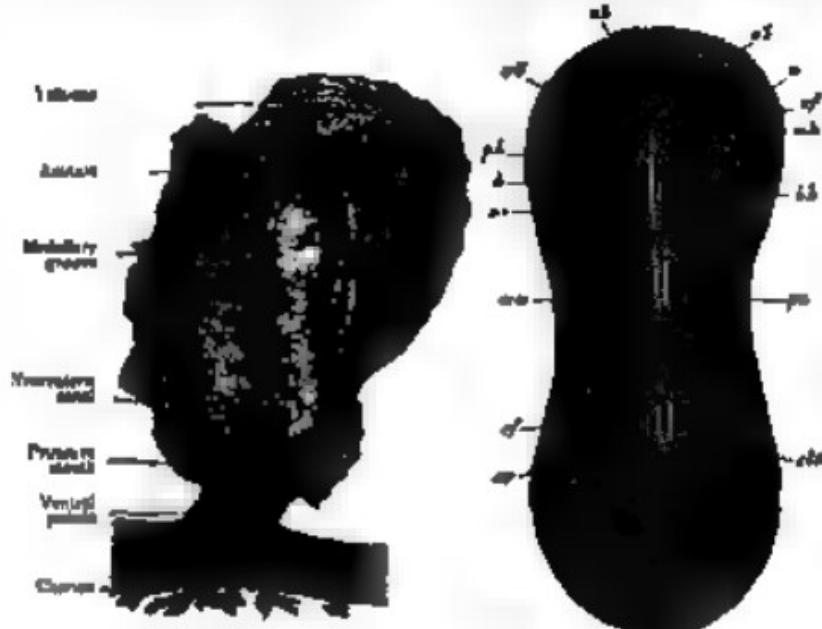


FIG. 135.

FIG. 135.—Human embryo at the neurulation stage, consisting of an oral head, from the tail of the neural tube developed two brachial arms (From Graw's *Atlas*).

FIG. 136.—Human embryo at the stage of 15 days. (From Goldfarb.) (Blackened areas above and below the head and neck are areas of protective respiration). In contrast to the dorsal view of pallid areas of protective respiration, in the ventral view, in the epibranchial area, in eye-region, in fore-brain, and middle-brain, the head-brain has protective regions for respiration.

gives from the open dorsal fissure, the upper cleft of which becomes narrower and narrower, a closed cylindrical tube (Fig. 137 *av*). This is one of the most important; it is the beginning of the central nervous system, the brain and spinal marrow, the medullary tube. This embryonic fact was formerly looked upon as very mysterious. We shall see presently that in the light of the theory of

the outer germinal layer, and is surrounded by the middle parts of the protomesoblast forced inwards (Fig. 146). The remaining portion of the skin-sense layer (Fig. 93 *A*) is now called the homoplasia or horn-layer; because from it is developed the whole of the outer skin or epidermis, with all its horny appendages (nails, hair, etc.).

A totally different organ, the *gastro-*

(primitive kidney) duct (*mag.*), is found to be developed at an early stage from the ectoderm. This is originally a quite simple, tube-shaped, lengthy duct, or straight canal, which runs from front to rear at each side of the proventerous (or the outer) side, Fig. 93 (*mag.*). It origi-

the first trace of it does not come from the skin-mesoe layer, but the skin-fibro layer.

The inner germinal layer, or the guttulae layer (Fig. 93 *sd.*), remains unchanged during these processes. A little later, however, it shows a quite flat, groove-like depression in the middle line

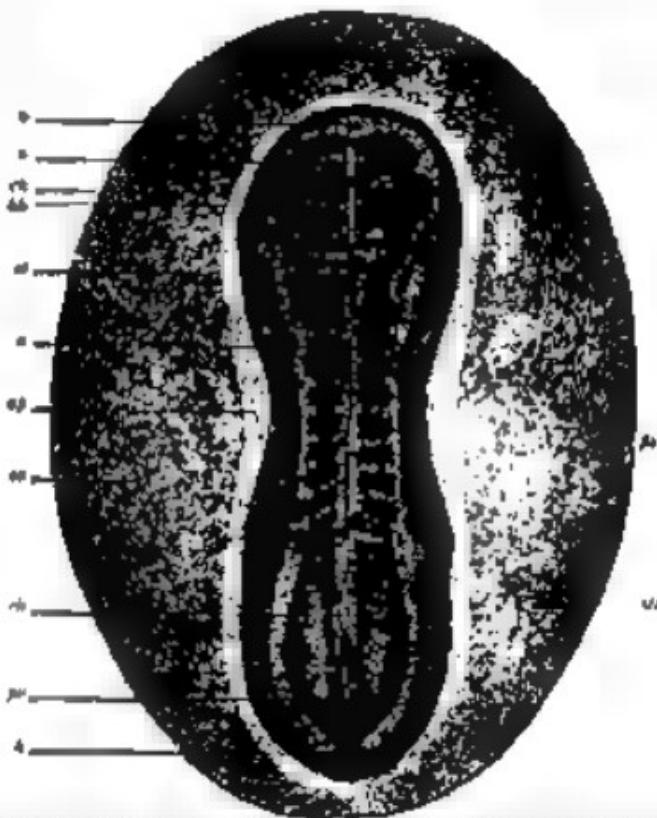


FIG. 93.—Mid-dorsal longitudinal section of an embryo of *Ambystoma* (Reddening), three days old. (Three slides.) Black line from above is the mid-dorsal or dorsal canal (with right parts of primitive epiphysis, the neural or ventral canal of primitive epiphysis, and the nervous system); the body of the heart, + fore-end & hind-end. In the median line we see the chorda /ad./ through the hypopharyngeal tube /mag./ = primitive segment, for passing through the primitive mouth.

gates, it seems, out of the horn-plate at the side of the medullary tube, in the gap that we find between the proventerous and the lateral plates. The proventer duct is visible in this gap and at the time of the severance of the medullary tube from the horn-plate. Other observers think that

it leaves the endoderm shield, directly under the chondro. This depression is called the gastric groove or furrow. This at once indicates the future sit of this germinal layer. As this ventral groove gradually deepens, and its lower edges bend towards each other, it is forced into a closed tube.

the alimentary canal, in the same way as the mandibular groove grows into the mandibular tube. The gut-layer (Fig. 137A), which lies on the gut-gland layer (78), naturally follows it in its folding. Moreover, the incipient gut-wall invaginates from the front of two layers, internally the gut-gland layer and externally the gut-layer.

The formation of the alimentary canal resembles that of the mandibular tube to this extent—in both cases a straight groove or furrow arises first of all in the middle line of a flat layer. The edges of this furrow then bend towards each other, and join to form a tube (Fig. 137). But the two processes are really very different. The mandibular tube closes in its whole length, and forms a cylindrical tube, whereas the alimentary canal remains open in the middle, and its ends continue for a long time in connection with the walls of the embryonic vesicle. The open connection between the two cavities is only closed at a very late stage, by the construction of the buccal. The closing of the mandibular tube is effected from both sides, the edges of the groove joining together from right and left; but the closure of the alimentary canal is not only effected from right and left, but also from front and rear; the edges of the radial groove growing together from every side towards the rear. Throughout the three higher classes of vertebrates the whole of this process of the construction of the gut is closely connected with the formation of the head, or with the separation of the embryo from the yolk-sac or yolkless vesicle.

In order to get a clear idea of this, we must understand carefully the relations of the embryo with the germinative area and the embryonic vesicle. This is done best by a comparison of the five stages which are shown in longitudinal section in FIGS. 138-142. The embryonic shield (a), which at first projects very slightly over the surface of the germinative area, soon begins to rise higher than b, and to separate from the vesicle over a wide area. At this point the ectodermic shield, located at some distance from the dorsal surface, shows still the original epiboly membrane (Figs. 138-139). We do not yet see any trace of articulation into head, neck, trunk, etc., or limbs. But the ectodermic shield has increased greatly in thickness, especially in the posterior part. It now has the appearance

of a thick, oval swelling, strongly curved over the surface of the germinative area. It begins to cover completely from the embryonic vesicle, with which it is connected at the ventral surface. As this process proceeds, the back bends more and more; in proportion as the embryo grows the embryonic vesicle decreases, and at last it merely hangs as a small vesicle from the belly of the embryo (Fig. 140-141). In consequence of the growth-movements which cause this movement, a groove-shaped depression is formed at the surface of the vesicle, the *buccal furrow*, which surrounds the vesicle in the shape of a pie, and a circular muscle or disc (Fig. 140-141) is formed at the outside of this pie for the elevation of the contiguous parts of the germinative vesicle.

In order to understand clearly this important process, we may compare the embryo to a fortress with its surrounding



FIG. 138. Transverse sections of the embryo and of a yolk in the mid-line of the body, at the stage when the gut-gland layer, the gut-layer, and the muscle-shield have been formed. The yolk is the same in all the figures, but the position of the embryo varies according to the stage. At each of the stages (Figs. 138-142) the yolkless vesicle (the yolk) is shown in the lower right-hand corner. A dotted line (dotted line) A dotted line (dotted line) A dotted line (dotted line).

moat and trench. The ditch consists of the outer part of the germinative area, and reaches to an end at the point where the area passes into the vesicle. The important fact of the middle germinative layer that brings about the formation of the body-area spreads beyond the borders of the vesicle over the whole germinative area. At first this middle layer reaches as far as the germinative area, the whole of the rest of the embryonic vesicle consisting of the limiting edge of the two original limiting layers, the outer and inner germinative layers. Hence, as far as the germinative area extends the germinative layer which lies between the two plates we have already mentioned in it, the outer skin-like layer and the inner gut-layer. These two plates diverge considerably, a clear solid gathering between them (Fig. 140-141). The inner plate, the gut-layer, remains on the lower layer of the embryo-area (the gut-gland layer). The

cular plate, the skin-fibre layer. This close on the outer layer of the germinative area, or the skin-series layer, and separates together with this from the embryonic vesicle. From these two united outer plates is formed a continuous membrane. This is the circular mound that rises higher and higher round the whole embryo, and at last joins above it (Figs. 133-143 *ad*). To return to our illustration of the fortress, we must imagine the circular rampart to be successively high and towering far above the fortress. Its edges bend over like the eaves of an overhanging wall of rock that would enclose the fortress; they form a deep hollow, and at last join together above.

The original embryonic vesicle, starting the open belly of the embryo (Fig. 142 *ab*), in more advanced embryos, in which the gastric wall and the ventral wall are nearly closed, it hangs out of the ventral opening in the shape of a small vesicle with a stalk (Figs. 141, 142 *ab*). The more the embryo grows, the smaller becomes the vitelline (yolk) sac. At first the embryo looks like a small appendage of the large embryonic vesicle. Afterwards it is the yolk-sac, as the remainder of the embryonic vesicle, that seems a small pouch-like appendage of the embryo (Fig. 142 *dc*). It ceases to have any significance at the end. The very wide opening, through which the gastric cavity



FIG. 14.—Three diagrams showing the development of the embryonic disk of the higher vertebrates, to show the origin of the dorsal wall from the ventral wall. In Fig. 14 the yolk-sac is shown, and the embryonic vesicle is a large, thin-walled sac. In Fig. 14 the ventral wall (*ad*) and the dorsal wall (*dc*) are shown, but the intermediate wall and the rounded part are not yet formed. In Fig. 14 the intermediate wall (*dc*) and ventral wall (*ad*) are shown, and the dorsal wall (*dc*) is raised. All the open growths (*ad*, *dc*, *bc*) become closed walls. The greater lobes are derived walls. The latter form the main mass of the body. A small portion of the body, called the yolk-sac, is a separate sac, of small size, a yolk-sac vesicle. A dorsal wall, a ventral wall, a yolk-sac vesicle, a yolk-sac layer, a germinative layer, a primitive mesoderm, a germinative layer, a chorioblast layer.

In the end the fortress-like cavity within the hollow cast has been formed by the growth of the edges of this large rampart.

As the two outer layers of the germinative area thus rise in a fold above the embryo, and join above it, they come of that to form a spacious cavity-like sacculus about it. This sacculus takes the name of the germinative membrane, or water-membrane, or amnion (Fig. 144 *ad*). The embryo lies in a watery fluid, which fills the space between the embryo and the amnion, and is called the amniotic fluid (Figs. 142, 144 *ad*). We will deal with this remarkable formation and with the allantois later on (Chapter XV.). In front of the allantois the yolk-sac or umbilical vesicle (*ab*), the remainder of

at first communicates with the umbilical vesicle, becomes narrower and narrower, and at last disappears altogether. The rest, the small pit-like depression that we find in the developed man in the middle of the abdominal wall, is the spot at which the remainder of the embryonic vesicle (the umbilical vesicle) originally entered into the ventral cavity, and joined on to the growing gut.

The origin of the cervix coincides with the complete closing of the external ventral wall. In the amniotes the ventral wall migrates in the same way as the dorsal wall. Both are formed substantially from the skin-fibre layer, and externally covered with the horn-plate, the border section of the skin-series layer. Both come into

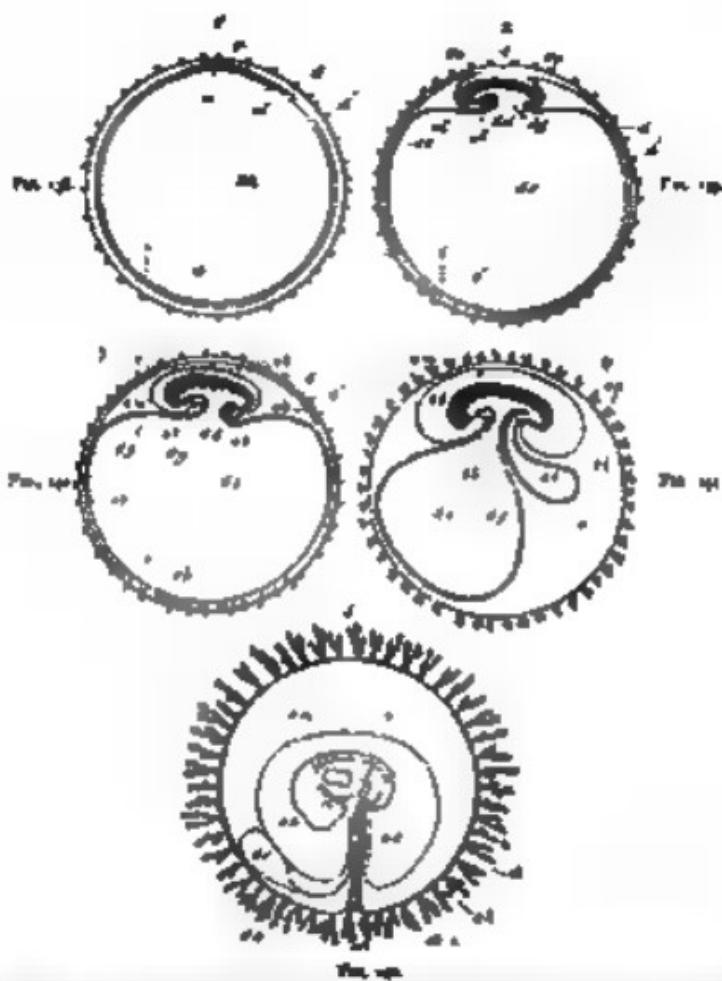


FIG. 13a-e.—Five diagrammatic longitudinal sections of the developing annelid embryo, all at the same magnification. In Fig. 13a, the longitudinal median process passes through the marginal or middle plate of the body, dividing the right and left halves; in Fig. 13b, the gut tube is seen from the left side. In Fig. 13c, the folded proboscis (*pro*) invaginates the gut tube, and the wall of the gut tube consists of the two primary layers. Between the outer (*ext.*) and inner (*int.*) layer the middle layer (*mid.*) has been developed in the region of the gynaecophore muscle. In Fig. 13d, the ectoderm (*ext.*) begins to separate from the mesoderm muscle (*mus.*), while the wall of the mesoderm muscle sheet is cut from its hindquarters, so that it looks like a thickened stalk. In Fig. 13e, the edges of the mesoderm (*ext.*) are pressed together over the neck of the proboscis, so that the mesoderm cavity (*mid.*); the endo-oesophagus disappears more completely from the mesoderm muscle (*ext.*). The gynaecophore muscle (*mus.*) is formed, both on the right and on the left, which the ultimate greater fold (*g. f.*). In Fig. 13e, the head (*cap.*) is simple, the proboscis (*pro.*) small, and the gut tube shows the beginning of the body wall; the coelom has formed between the mid-plate (*mid.*) and the body wall (*ext.*). The figure is a section of a later gynaecophore stage, in which the gut tube + outer gynaecophore layer, are visible. (The head, oesophagus, and proboscis have disappeared entirely, so that the shape of the animal is now a very simple, elongated, smooth, cylindrical body.) The figure is a section of a later gynaecophore stage, in which the gut tube + outer gynaecophore layer, are visible. (The head, oesophagus, and proboscis have disappeared entirely, so that the shape of the animal is now a very simple, elongated, smooth, cylindrical body.)

existence by the conversion of the two flat germinal layers of the embryonic shield into a double tube by folding from opposite directions; above, at the back, we have the vertebral canal which encloses

the closing in the middle of the dorsal wall take place in the same way as the medullary tube, which is henceforth enclosed by the vertebral tube. Thus is formed the dorsal wall, and the medullary tube takes up a position inside the body. In the same way the prevertebral mass grows afterwards round the chorda, and forms the vertebral column. Now thus the inner and outer edge of the prevertebral plate splits on each side into two horizontal plates, of which the upper passes between the chorda and medullary tube, and the lower between the chorda and myoseptal tube.

the medullary tube, and below, at the belly, the wall of the body-cavity which contains the alimentary canal (Fig. 157).

We will consider the formation of the dorsal wall first, and that of the ventral wall afterwards (Figs. 145-147). In the middle of the dorsal surface of the embryo there is originally, as we already know, the medullary tube directly beneath the horn-plate (h), from the middle part of which it has been developed; later, however, the prevertebral plates (*pv*) grow over from the right and left between these originally connected parts (Figs. 146, 146'). The upper and inner edges of the two prevertebral plates pass between the horn-plate and medullary tube, force these away from each other, and finally join between them in a split that corresponds to the middle line of the back. The consequence of these two dorsal plates and

as the plates meet from both sides above and below the chorda, they completely enclose it, and so form the tubular outer chondro-plate, the sheath from



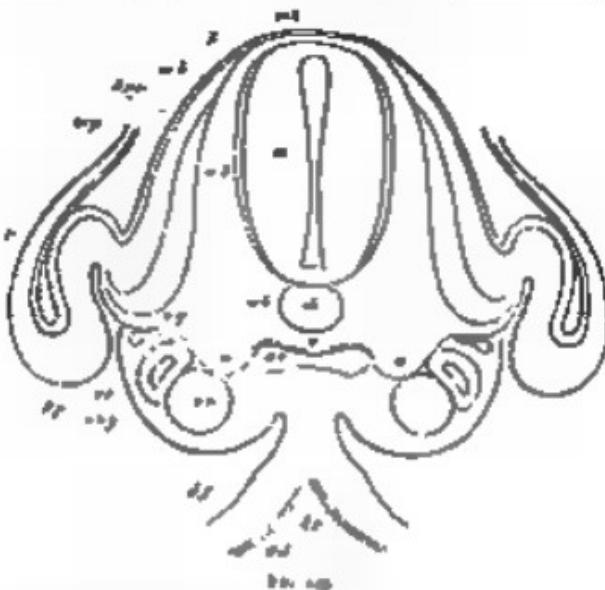
FIG. 153.—*Diagram illustrating the early stages of vertebral column formation.* Fig. 153 is of the second day of the chick. The head of the fore-brain, and Fig. 154 of the fifth day of incubation. The eye is shown separately, magnified about ten times. Fig. 155 is from a fourth day chick. The head is shown separately, a fore-brain, one medullary tube, one prevertebral plate, an epibranchial layer, an epibranchial muscle-plate, one prevertebral layer, an epibranchial layer, the chorda (here represented as a horizontal oval), a fore- and a fore-part of the spinal nerve, a fore- and a fore-part of the body-wall, a fore-part of the epibranchial layer, an epibranchial muscle, an epibranchial muscle, an epibranchial muscle, a fore-part of the epibranchial layer, an epibranchial muscle. In Fig. 155 the larger part of the right half, in Fig. 154 the larger part of the left half, of the embryo is omitted. Of the yolk-sac or remainder of the embryo remains only a small piece of the tail as indicated below.

which the vertebral column is formed (see chorda, Fig. 155 C, x; Figs. 145-147).

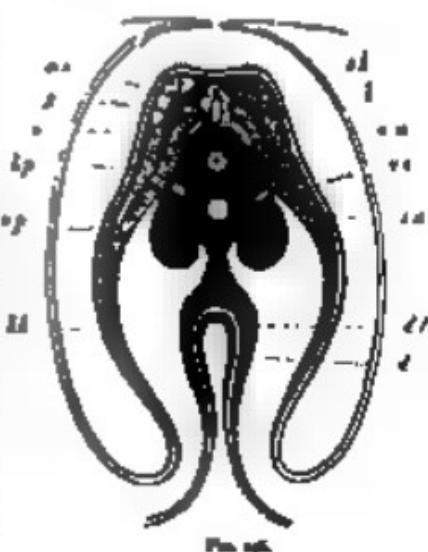
We find in the construction of the ventral wall precisely the same processes

as in the formation of the dorsal wall (Fig. 137 *B*, Fig. 144 *A*, Fig. 146 *A*). It is formed on the flat ectopharyngeal shield of the amnionites from the upper plates of the

polypore (Fig. 103). The external navel in this is the definitive point of the closing of the ventral wall; this is visible in the developed body as a small depression.



peripheral zone. The right and left peripheral plates bend downwards towards each other, and grow round the gut in the same way as the gut itself does. The outer part of the lateral plates forms the ventral wall in the lower wall of the body, the two lateral plates bending considerably on the inner side of the amniotic fold, and growing towards each other from right and left. While the alimentary canal is closing, the body-wall also closes on all sides. Hence the ventral wall, which encloses the whole ventral cavity below, consists of two parts, two lateral plates that bend towards each other. These approach each other all along, and at last meet at the navel. We ought, therefore, really to distinguish two navels, an inner and an outer one. The internal or intestinal navel is the definitive point of the closing of the gut wall, which puts an end to the open communication between the ventral cavity and the cavity of the



With the formation of the maternal navel and the closing of the allanto-uterine canal is connected the formation of two cavities, which we call the capital and the pelvic sections of the ventral cavity. As the embryonic shield lies flat on the wall of the embryonic vesicle at first, and only gradually separates from it, its fore and hind ends are independent in the beginning; on the other hand, the midline part of the ventral surface is connected with the yolk-sac by means of the vitelline or umbilical duct (Fig. 147 *a*). This leads to a notable curving of the dorsal surface, the head-end bends downwards towards the breast and the tail-end towards the

buttocks. As a result of these processes the embryo attains a shape that may be compared to a wooden shoe, or, better still, to an overturned canoe. Imagine a canoe or boat with both ends rounded and a small covering before and behind; if this canoe is turned upside down, so that the curved bow is uppermost, we have a fair picture of the canoe-shaped embryo (Fig. 147). The upturned convex keel corresponds to the midline line of the back; the small chamber underneath the fore-deck represents the capital cavity, and the small chamber under the rear-deck the pelvic chamber of the gut (cf. Fig. 148).



FIG. 147.—Sagittal longitudinal section of the embryo of a chick (day of incubation 1), seen from the right side (from left to the left). Dorsal body dark, with central hollow of gut; a small lobe of yolk-sac is lying immediately anterior of the heart; a portion of the heart; 3 with the uterine / oviduct / allanto-uterine canal (left); 4 with the oviduct; 5 yolk-sac; 6 yolk; 7 vitelline duct; 8 amniotic cavity; 9 yolk-sac cavity; 10 amniotic cavity; 11 yolk-sac; 12 allanto-uterine canal; 13 uterine cavity; 14 yolk-sac cavity; 15 amniotic cavity; 16 yolk-sac; 17 allanto-uterine canal; 18 uterine cavity; 19 yolk-sac cavity; 20 amniotic cavity; 21 yolk-sac; 22 allanto-uterine canal; 23 uterine cavity; 24 yolk-sac cavity; 25 amniotic cavity; 26 yolk-sac; 27 allanto-uterine canal; 28 uterine cavity; 29 yolk-sac cavity; 30 amniotic cavity.

belly. We see this very clearly in the excellent old disaognostic illustration given by Baer (Fig. 147), a median longitudinal section of the embryo of the chick, in which the dorsal body or epidermis is deeply shaded. The embryo seems to be trying to roll up, like a hedgehog protecting itself from its partner. This pronounced curve of the back is due to the more rapid growth of the convex dorsal surface, and is directly connected with the severance of the embryo from the yolk-sac. The further bending of the embryo leads to the formation of the "head-cavity" of the gut (Fig. 147, above 2) and a similar one at the tail, known as its "pelvic cavity."

The embryo now, as it were, presses into the outer surface of the embryonic vesicle with its free ends, while it moves away from it with its middle part. As a result of this change the yolk-sac becomes bidental; only a pouch-like outer appendage at the middle of the ventral wall. The ventral appendage, growing smaller and smaller, is afterwards called the umbilical (navel) vesicle. The cavity of the yolk-sac or umbilical vesicle communicates with the surrounding visceral cavity by a wide opening, which gradually contracts into a narrow and long canal, the vitelline (yolk) duct (*ductus vitellinus*, Fig. 147 *a*). Hence, if we were to imagine ourselves in

the cavity of the yolk-sac, we could get from it through the yolk-sac into the midline and still wide open part of the alimentary canal. If we were to go forward from there into the head-part of the embryo, we should reach the capillary cavity of the gut, the fore-end of which is closed up.

The reader will ask: "Where are the mouth and the anus?" These are not at first present in the embryo. The whole of the primitive gut-cavity is completely closed, and is merely connected in the midline by the vitelline duct with the equally closed cavity of the embryonic vesicle (Fig. 141). The two later apertures of the alimentary canal—the anus and the mouth—are secondary constructions, formed from the outer skin. In the hind-gut, at the spot where the mouth is found subsequently, a pit-like depression is formed, and this grows deeper and deeper, pushing towards the blind fore-end of the capillary cavity; this is the mouth-pit. In the same way, at the spot in the outer skin where the anus is afterwards situated a pit-shaped depression appears, grows deeper and deeper, and approaches the blind hind-end of the pelvic cavity, this is the anato-pit. In the end these pits touch with their deepest and innermost points the two blind ends of the primitive alimentary canal, so that they are now only separated from them by thin membranous partitions. These membranes finally disappear, and henceforth the alimentary canal opens at front as the mouth and in the rear by the anus (Figs. 142, 147). Hence at first, if we penetrate into these pits from without, we find a partition cutting them off from the cavity of the alimentary canal, which gradually disappears. The formation of mouth and anus is secondary to all the vertebrates.

During the important processes which lead to the formation of the neck, and of the intestinal wall and ventral wall, we find a number of other interesting changes taking place in the embryonic shield of the annelids. These relate chiefly to the proventral ducts and the first blood-vessels. The proventral (primitive kidney) ducts, which at first lie quite flat under the hæmaphilic or spiderm (Fig. 91 *see*), now back towards each other in consequence of special growth movements (Figs. 143-

145 *see*). They depart more and more from their point of origin, and approach the gut-gland layer. In the end they lie deep in the interior, on either side of the mesenteric, underneath the chords (Fig. 145 *see*). At the same time, the two proventral aortas change their position (cf. Figs. 138–145 *so*): they trend forwards underneath the chords, and these coalesce at last to form a single mesenteric aorta, which is found under



The fig.-diagrammatic sections of the fore half of a *caecum-polydora*; at the end of the fore day of segmentation from the 16th inst. A hæmaphilic or spiderm is in the blind fore-end of the ventral side (Fig. 141); below it is the capillary cavity of the gut, of which the floor is the gut-gland layer. A hæm-plate, at nearly the middle of the body, is indicated, as is also the coelom. (From Girard.)

the midventerous vertebral column (Fig. 145 *so*). The cardinal veins, the first venous blood-vessels, also back towards each other, and eventually unite immediately above the rudimentary kidneys (Figs. 145 *so*, 146 *see*). In the same spot, at the same side of the fore-kidneys, we soon see the first trace of the sexual organs. The most important part of this apparatus (except from all its appendages) is the ovary in the female and the testicle

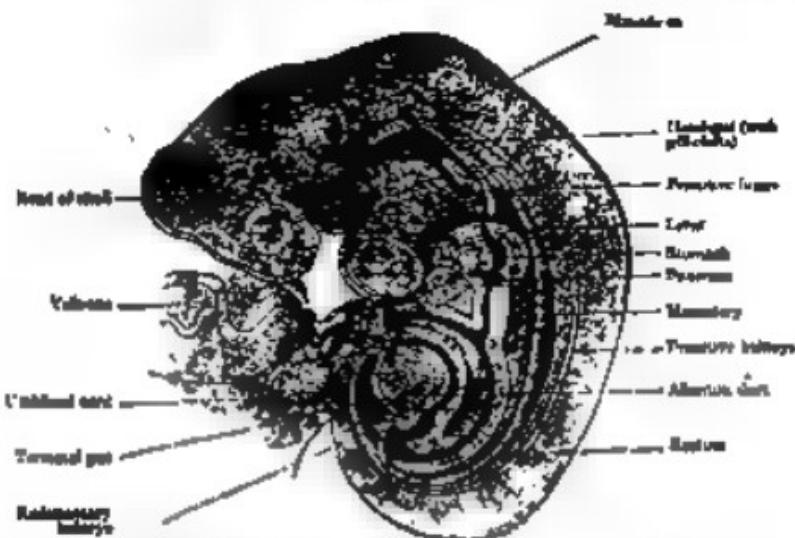


FIG. 140.—Transverse section of a leech embryo at the fourth week, viewed at an angle long enough to show the coelom.



FIG. 141.—Transverse section of a leech embryo at the fifth week. The mouth, pharynx, oesophagus, and midgut show the characteristic form of the alimentary canal. The Malpighian tubules, the allantois, and the vagina are also clearly defined.

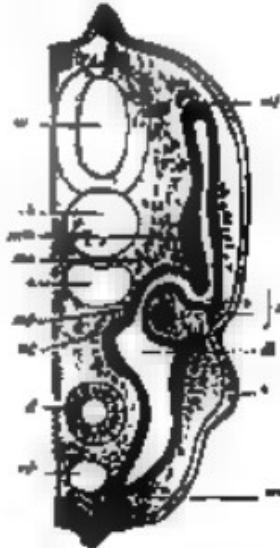


FIG. 142.—Transverse section of a leech embryo at the young hatching stage. The alimentary tube is clearly seen, as are the Malpighian tubules, the allantois, and the ventral nerve of the nervous system, which passes through the middle plate of the proventriculus. It is particularly a feature of the nervous system that the ganglion cells are given off before the epiphysis and supra-oesophageal ganglion.

In the male. Both develop from a small part of the cell-lining of the body-cavity, at the spot where the skin-fibre layer and gut-fibre layer touch. The connection of

this embryonic gland with the proventricular ducts, which lie close to it and assume most important relations to it, is only secondary.

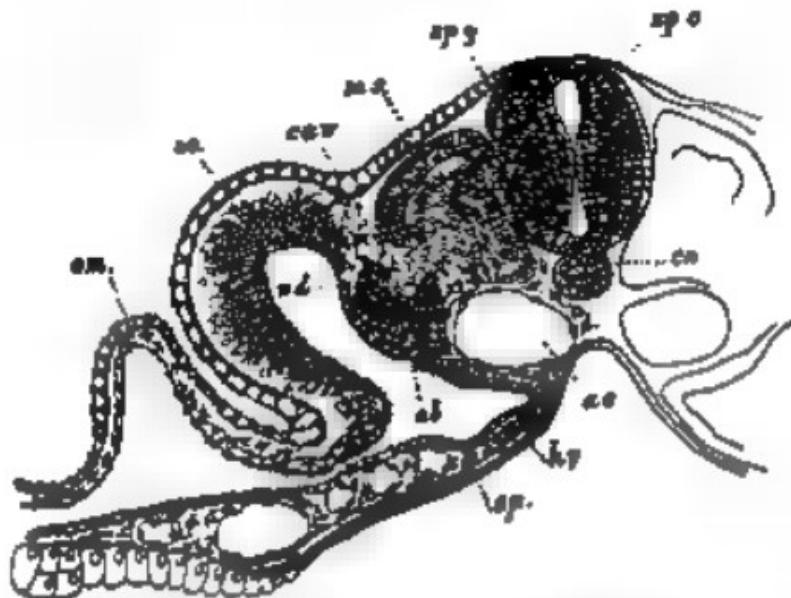


FIG. 154.—Transverse section of a developing bird, transversely through proventriculus and heart. (From Pöhl.) From a dorsal lateral part of the median body, just in front of the heart, a thick cell-lining, a bit like the horn-plate, of muscle or double nerve, is detached from the gut-lining, with blood-vessels in common, and nearly plain, on the dorsal wall of the proventriculus (below the cardiac vein *C. V.*) in the proventricular duct (*P. D.*) and a large well-defined vessel (*V. P.*). The skin-fibre layer of the body-wall (*S. F.*) is continuous with the proventricular duct (*P. D.*) and the anterior splanchnic artery and the structures derived from them (there is formed early an extensive network with certain cells and nervous structures) (lettering = "embryology").

## CHAPTER XIV.

### THE ARTICULATION OF THE BODY<sup>1</sup>

The vertebrate stem, to which our race belongs as one of the latest and most advanced outcomes of the natural development of life, is slightly placed at the head

of the animal kingdom. This privilege cannot be succeeded to it, not only because man stands in point of fact over far above all other animals, and has been fitted to

<sup>1</sup> The term "articulation" is used in this chapter to denote both "synapsis" and "synostosis" in the ordinary sense—Trotter.

the quality of "body of motion"; but also between the vertebrates organized for movement all the other characteristics, also, in complexity of structure, and in the advanced character of its functions. From the point of view of both anatomy and physiology, the vertebrates stand unique all the other, or invertebrate, animals.

There is only one among the two classes of the animal kingdom that can in many respects be compared with the vertebrates, and reaches an equal, if not a greater, importance in every point. This is the class of the arthropods, composed of three classes: 1, the annelids (annelines, leeches, and segmatoform); & the crustaceans (crabs, etc.); 2, the trilobites (trilobites, trilobites, etc.). The class of the articulates is superior not only to the vertebrates, but to all other invertebrates, in variety of form, number of species, distinctness of individuals, and general importance in the economy of nature.

When we have thus divided the vertebrates and the articulates to be the most important, and most advanced, of the twelve classes of the animal kingdom, the question arises whether this special position is deserved by them on the ground of a peculiarity of organization that is common to the two. The answer is that this is really the case; it is clearly expressed in *Crustacean articulation*, which we may briefly call *articulation*. In all the vertebrates and articulates the developed individual consists of a series of successive numbers (segments or somites—“parts”); in the vertebrates these are called primitive segments or somites. In each of these segments we find a small group of organs arranged in the same arrangement, so that we may regard each segment as an individual unity, or a special “individual” subordinated to the entire personality.

The similarity of their segmentation, and the consequent physiological advance in the two classes of the vertebrates and articulates, has led to the assumption of a direct affinity between them, and an attempt to derive the former directly from the latter. The vertebrates were supposed to be the direct ancestors, not only of the crustaceans and trilobites, but also of the vertebrates. We shall see later (Chapter XX.) that this ancestral theory of the vertebrates is entirely wrong, and leaves the most important difference in the organization of the two classes. The basal organization of the vertebrates is

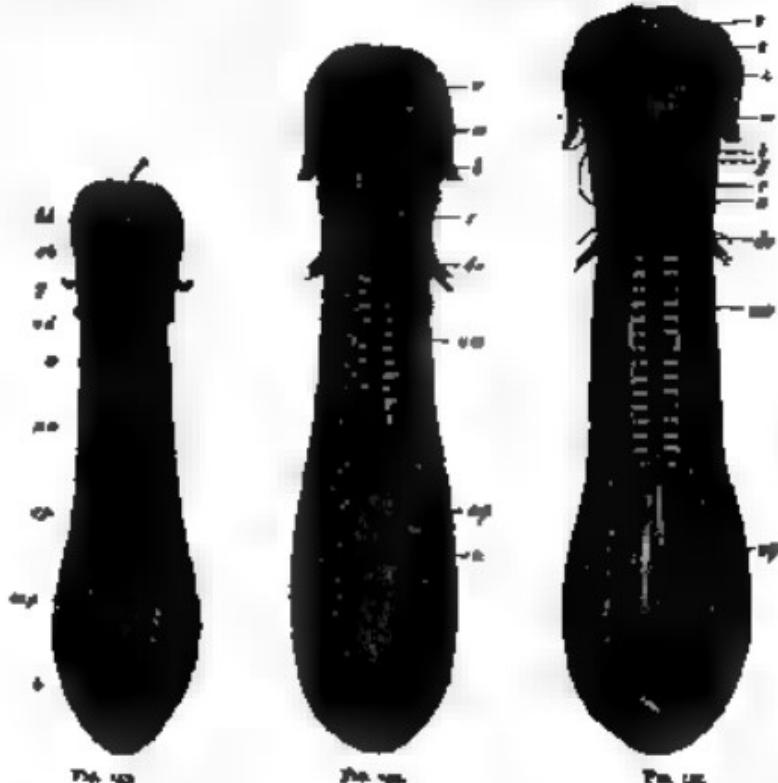
just as profoundly different from the external organization of the articulates as are their distinct structures, nervous system, muscular system, and so on. The articulates have been developed in a totally different way in the two cases. The articulated class (Figs. 83-86), which we have compared to one of the chief palaeozoic embryonic forms of the vertebrate group, and from which we have inferred the existence of a corresponding ancestral form for all the vertebrates and trilobites, is quite uncharitable as the end-form of the articulates.

All articulated animals arose originally from what-called state. This principle is as firmly established as the paleontological fact that every articulated animal-form develops from an unsegmented embryo. But the organization of the embryo is totally different in the two states. The characteristic of all the vertebrates is determined by the dorsal musculature, the respiratory cavity, which passes at the primitive epoch in the embryonic state, and the axial muscle, but both the two. None of the articulates, either annelids or arthropods (trilobites and sea-hares), show any trace of this type of organization. Moreover, the development of the chief systems of organs proceeds in the opposite way in the two states. Never the organization must have arisen independently in each. This is not at all surprising; we find homologous cases in the multicellularization of the higher plants, and in several groups of other animal forms.

The characteristic internal articulation, of the vertebrates and its importance in the organization of the state are well known in the study of the skeleton. Its chief and central part, the vertebration or bony vertebral column, affords no obvious instance of vertebrate organization; it consists of a series of cartilaginous or bony plates, which have long been known as vertebral (or spooly). Each vertebra is directly connected with a special section of the muscular system, the nervous system, the vascular system, etc. Thus most of the “animal organs” take part in this vertebration. But we see, when we were considering our first vertebrate character (in Chapter XI.), that the same internal articulation is also found in the lowest primitive vertebrates, the annelids, although here the whole skeleton consists entirely of the simple discs, and do not at all articulate.

Hence the articulation does not proceed primarily from the skeleton, but from the muscular system, and is clearly determined by the more advanced undulating movements of the primitive cleithrognathians.

"metameres" or primitive segments to those so-called "primitive vertebrae." If the latter name is retained at all, it should only be used of the sclerites—the small part of the annulus from which the later vertebrae class actually develop.



FIGS. 142-144.—Side-viewed embryological stage of the elasmodermatheca, in three successive stages of development, viewed at first the dorsal surface, ventral view, and then the ventral surface. The 142 year-old specimen is a larva of about 1 mm. long; 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189, 190, 191, 192, 193, 194, 195, 196, 197, 198, 199, 200, 201, 202, 203, 204, 205, 206, 207, 208, 209, 210, 211, 212, 213, 214, 215, 216, 217, 218, 219, 220, 221, 222, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 277, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297, 298, 299, 300, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 327, 328, 329, 330, 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1394, 1395, 1396, 1397, 1398, 1399, 1391, 1392, 1393, 1394, 1395, 1396, 1397, 1398, 1399, 1400, 1401, 1402, 1403, 1404, 1405, 1406, 1407, 1408, 1409, 1401, 1402, 1403, 1404, 1405, 1406, 1407, 1408, 1409, 1410, 1411, 1412, 1413, 1414, 1415, 1416, 1417, 1418, 1419, 1411, 1412, 1413, 1414, 1415, 1416, 1417, 1418, 1419, 1420, 1421, 1422, 1423, 1424, 1425, 1426, 1427, 1428, 1429, 1421, 1422, 1423, 1424, 1425, 1426, 1427, 1428, 1429, 1430, 1431, 1432, 1433, 1434, 1435, 1436, 1437, 1438, 1439, 1431, 1432, 1433, 1434, 1435, 1436, 1437, 1438, 1439, 1440, 1441, 1442, 1443, 1444, 1445, 1446, 1447, 1448, 1449, 1441, 1442, 1443, 1444, 1445, 1446, 1447, 1448, 1449, 1450, 1451, 1452, 1453, 1454, 1455, 1456, 1457, 1458, 1459, 1451, 1452, 1453, 1454, 1455, 1456, 1457, 1458, 1459, 1460, 1461, 1462, 1463, 1464, 1465, 1466, 1467, 1468, 1469, 1461, 1462, 1463, 1464, 1465, 1466, 1467, 1468, 1469, 1470, 1471, 1472, 1473, 1474, 1475, 1476, 1477, 1478, 1479, 1471, 1472, 1473, 1474, 1475, 1476, 1477, 1478, 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middle of the salivary-shaped embryonic shield, several pairs of dark squares appear, symmetrically distributed on both sides of the chords (Figs. 121-123). Transverse sections (Fig. 123 *en face*) show that they



FIG. 120.—Embryo of the chick, sixteen hours old, the first ten head-chorda segments and a portion of the trunk showing the first four pairs of somites, which appear out of the field of segmentation, so that the first segment is a median line, 7 anterior, + posterior, + first segment.

belong to the sclerotoma (epineurium) of the myelomere, and are separated from the parietal zone (myoseptum) by the lateral folds, in section they are well quadrangular, almost square, so that they look something like dice. These pairs of "cubes" of the myelomere are the first traces of the primitive segments or somites, the so-called "protovertebrates" (Figs. 124-126 *en face*).

Among the mammals the embryos of the marsupials have three pairs of somites (Fig. 127) after forty hours, and eight pairs after seventy-two hours (Fig. 128). They develop more slowly in the embryos of the rabbit; this has three somites on the eighth day (Fig. 129), and eight somites a day later (Fig. 130). In the incubated hen's egg the first somites make their appearance thirty hours after incubation begins (Fig. 131). At the end of the second day the number has risen to sixteen or eighteen (Fig. 132). Articulation of the somites, to which the somites are their origin,

proceeds serially from front to rear, new transverse constrictions, of the "protovertebral plates," forming continuously and successively. The first segment, which is almost half-way down in the embryonic shield of the amniote, is the foremost of all; from this first somite is formed the first cervical vertebra with its meniscal and interclavicular parts. It follows from this, firstly, that the multiplication of the primitive segments proceeds backwards from the front, with a constant lengthening of the hinder end of the body, and, secondly, that at the beginning of segmentation nearly the whole of the anterior half of the salivary-shaped embryonic shield of the amniote belongs to the head-half, while the whole of the rest of the body is formed from the hinder half. We are reminded that in the amphioxus (and in our hypothetical primitive vertebrate, Figs. 128-132) nearly the whole of the fore half corresponds to the head, and the hind half to the trunk.

The number of the metaplaeni, and of the embryonic vertebrae or primitive segments from which they develop, is also considerable. In the vertebrates, according as the hind part of the body is short or is lengthened by a tail, so the developed spine (including the rudimentary tail) consists of thirty-three vertebrae, the solid corpus of which is formed by that number of vertebrae in the articulated column (seven cervical, twelve dorsal, five lumbar,

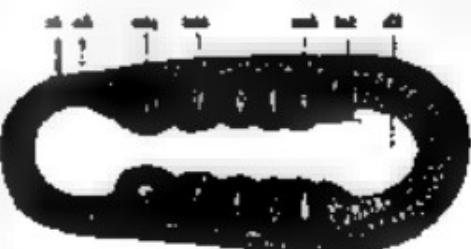


FIG. 121.—Embryo of the chick, twenty hours old, with all the somites, shown now, for the first time, articulated. 1, ante.; 2, head; 3, abd.; 4, thorac.; 5, and ventr. layers; 6, clavicular canal; 7, median line; 8, dorsal myoseptum; 9, posterior-ventral line; 10, head (and foremost) median segment.

five sacral, and four caudal). To these we must add at least nine head-vertebrae which originally (in all the craniota) constitutes the skull. Thus the total number of the primitive segments of the amniote

body is raised to at least forty-five; it would reach forty-five to forty-eight if (according to recent investigations) the number of the original segments of the skull is put at twelve to fifteen. In the tailless or anelopod apes the number of metameres is much the same as in man, only differing by one or two; man is much larger in the long-tailed apes and most of the other mammals. In long apes and fishes it reaches several hundred (sometimes 400).

modified embryonic processes of the coelom. The articulation of the amphioxus begins at an early stage—earlier than in the craniates. The two coelom-pouches have hardly grown out of the primitive gut (Fig. 156 c) when the blind fore part of it (farthest away from the primitive mouth, a) begins to separate by a craniopharyngeal fold (*x*): this is the first primitive segment. Immediately afterwards the blind part of the coelom-pouches begins to divide into a series of pouches by

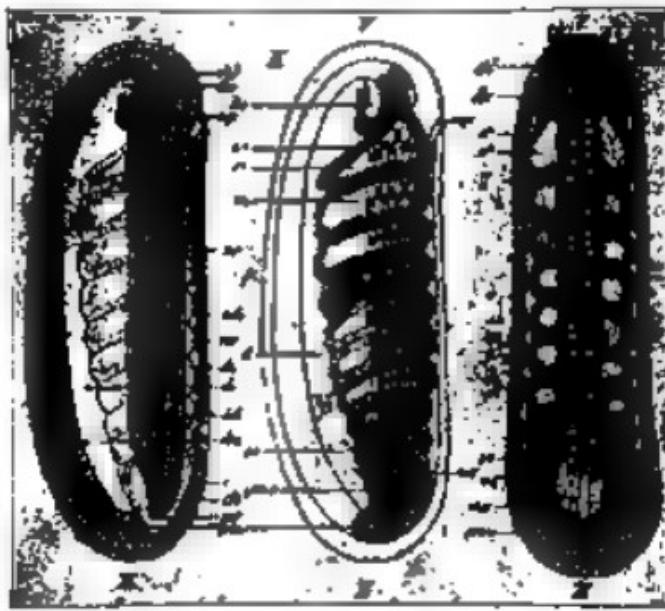


FIG. 156.

FIG. 157.

FIG. 158.

FIGS. 156-158.—Development of the amphioxus. Twenty-four hours old, with eight segments. (Frog No. 1.) FIGS. 157 and 158 between two hours old. FIG. 156 shows head region, in which only the nucleus of the eight primitive segments is recognizable. FIG. 157 shows coelom and coelom-pouches. First fold of head and of gut, the anterior and old upper part of the gut, the coelom, the coelom-pouches, the ventral, the dorsal half of the overall tube, epibranchial groove, the first pouch of the gut, all coelom, and coelom-pouch-fold, the older coils of the coelom-pouches.

In order to understand properly the real nature and origin of articulation in the human body and that of the higher vertebrates, it is necessary to compare it with that of the lower vertebrates, and bear in mind always the genetic connection of all the members of the stem. In this the simple development of the humble amphioxus once more furnishes the key to the complex and congenitally

new however folds (Fig. 157). The first fold of these primitive segments (or *a*) is the first and oldest; in Figs. 157 and 158 there are already five formed. They separate so rapidly, one behind the other, that eight pairs are formed within twenty-four hours of the beginning of development, and seventeen pairs twenty-four hours later. The number increases as the embryo grows and extends

backwards, and new cells are formed constantly (at the primitive mouth) from the two primitive mesodermic cells (Figs. 255-260).

This typical articulation of the two coelom-sacs begins very early in the lancelet, before they are yet severed from the primitive gut, so that at first each segment-cavity (*as*) still communicates by a narrow opening with the gut, like an intestinal gland. But this opening soon closes by complete severance, proceeding regularly backwards. The closed

segment-section, to the prosencephalic, primitive-diencephalic canals, and from thence to the segmental rudiments of the spinal glands or gonads. The portion of the muscular dorsal plates (*myotome*-canals), and determine the permanent articulation of the vertebrate organism. But the partitions of the large ventral plates (*mesotomes*) become thinner, and afterwards disappear in part, so that the canals run together to form the metapleural or the simple permanent body-cavity.

The articulation proceeds in all



FIG. 255.

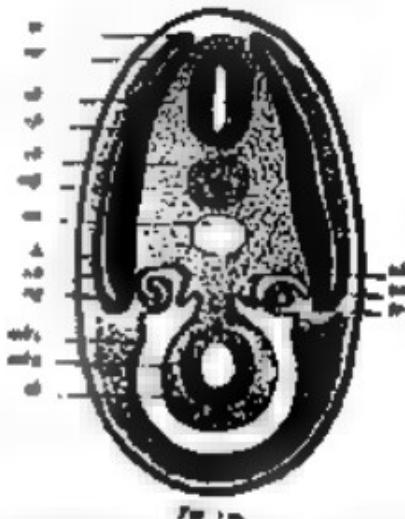


FIG. 256.

FIGS. 255 AND 256.—Transverse sections of lancelets, showing through the region of the buccal cavity. (Fig. 255, at the earliest stage of coelom-formation; Fig. 256, at a slightly advanced stage.) In both cases they are enclosed in a thin outer skin-layer, or covered with a thin, not membranous, skin, or part of the body-wall, of mesoderm, of ectoderm, or a mixture of both (mesoectoderm). In both figures, label 'g' = gut; label 'as' = segmental sacs; label 'm' = mouth; label 'v' = ventral plate; label 'p' = middle plate; label 'l' = lateral plate; label 'n' = nerve-fibres (spinal nerves).

segments then extend rearwards, so that their upper half grows upwards like a fold between the endostome (*ad*) and neural tube (*n*), and the lower half between the endostome and alimentary canal (*as*; Fig. 255, left half of the figure). Afterwards the two halves completely separate, a lateral longitudinal fold cutting between them (left, right half of Fig. 256). The dorsal segments (*ad*) provide the muscles of the trunk the whole length of the body (Fig. 256); this cavity afterwards disappears. On the other hand, the ventral parts grow also, from their

extremity the same way in the other vertebrates, the craniota, starting from the coelom-pouches. But whereas in the former case there is first a transverse division of the coelom-sac (by vertical folds) and then the dorso-ventral division, the procedure is reversed in the craniota; in their case each of the long coelom-pouches first divides into a dorsal (primitive segment plates) and a ventral (lateral plates) section by a lateral longitudinal fold. Only the former are then broken into primitive segments by the subsequent vertical folds; while the latter (segmental

for a time in the amphioxus) remains undivided, and, by the divergence of these parietal and visceral plates, form a body-cavity that is unified from the front. In this case, again, it is clear that we must regard the features of the young larva as ontogenetically modified processes that can be traced paleogenetically in the older larva.

We have an interesting intermediate stage between the scrana and the fishes in these and many other respects in the cyclostoma (the hag and the lamprey, cf. Chapter XXI.)

Among the fishes the teleostii, or primitive fishes, yield the most important information on these and many other phylogenetic questions (Figs. 16a, 16b). The careful studies of Rückert, Van Wybe, H. R. Ziegler, and others, have given us most valuable results. The products of

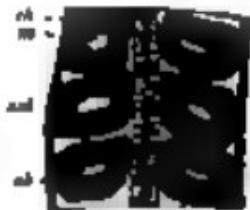


Fig. 16a.—Primitiv (neurula) doppelseitiges Modell eines Teleosteaner mit den drei primären Myomeren. A) dorsale, B) ventrale, C) laterale Myomere.

the middle germinal layer are partly clear in these cases at the period when the dorsal primitive segment cavities (or myomeres, A) are still connected with the ventral body-cavity (B; Fig. 16a). In Fig. 16b, a somewhat older embryo, these cavities are separated. The outer or lateral wall of the dorsal myomere yields the cartilage-plate (*cp*), the foundation of the connective cartilage. From its inner or median wall are developed the muscle-plates (*mp*), the radicles of the transversal muscles and the skeletal plates, the framework of the vertebral column (*sk*).

In the amphibia, also, especially the water-salamander (*Triton*), we can observe very clearly the articulation of the coelom-pouches and the rise of the primitive segments from their dorsal bulk (cf. Fig. 91, A, B, C). A horizontal longitudinal section of the amphibian embryo (Fig. 16c) shows very clearly the

series of pairs of these vertebral dorsal segments, which have been cut off on each side from the ventral side-plains, and to the right and left of the chords.

The segmentation of the annelites agrees in all essential points with that of the



Fig. 16b.



Fig. 16c.

Fig. 16a.—Die dritte cervical vertebra (fische).  
Fig. 16b.—Die sechste dorsal vertebra (fische).

three former classes of vertebrates we have considered; but it varies considerably in detail, as consequence of ontogenetic disturbances that are due in the first place (like the degeneration of the rectal-pouches) to the large development of the fore-gut. As the pressure of this seems to force the two middle layers together from the start, and as the solid structure of the mesoderm apparently loses the original hollow character of the mes., the two sections of the mesoderm, which are at that time divided by the lateral fold—the dorsal segment-plains and ventral side-plains—have the appearance at first of solid layers of cells (Figs. 16d–g). And when the articulation of the somites begins in the cube-shaped embryonic shield, and a couple of proto-somites are developed in succession, constantly increasing in number towards the rear,



Fig. 16d.—Die zweite lumbale vertebra (amph.).

these cube-shaped somites (formerly called proterosomites, or primitive vertebrae) have the appearance of solid dice, made up of monolete cells (Fig. 93). Nevertheless, there is for a time a ventral cavity, even in these solid

"proterovertebrates" (Fig. 143 *med.*). This vesicular condition of the provertebrates is of the greatest phylogenetic interest; we must, according to the colobon theory, regard it as an hereditary reproduction of the hollow dorsal sacculae of the amphioxus (Figs. 156-160) and the lower vertebrates (Figs. 167-169). This rudimentary "provertebral cavity" has no physiological significance whatever in the amphioxo-anellidines; it soon disappears, being filled up with cells of the mesodermic state.

The interview reading part of the

divides into two plates, which grow round the chorda, and thus form the foundation of the body of the vertebrate (Fig. 137). The upper plate presses between the chorda and the rudimentary tube, the lower between the chorda and the alimentary canal (Fig. 137 C). As the plates of two opposite provertebral pieces unite from the right and left, a circular sheath is formed round this part of the chorda. From this develops the body of a vertebrate—that is to say, the mesenteric source or central bulk of the being, which is called the "vertebra."



For my friend of a short-temper (Antonius), author of an anti-long-musique (Nelly Lutz) (From Verdi's "Don Giovanni" - See also the next note)

primitive segment plates, which lie immediately on the *chaetae* (Fig. 145 ab) and the median laryngeal tube (*ml*), form the vertebral column in all the higher vertebrates (*ml* is wanting in the lower); hence it may be called the *vertebral plate*. In such of the proterostomes it is called the "sclerotonous" (in opposition to the underlying muscular plate, the "myotomous"). From the phylogenetic point of view the myotomes are much older than the sclerotonous. The lower or ventral part of each sclerite (the inner and lower edge of the cube-shaped proterostome)

proper and transverse, the medullary tube (Figs. 145-146). The upper or dorsal limb of this bony ring, the vertebral arch (Fig. 145 red), arises in just the same way from the upper part of the apical plate, and therefore from the inner and upper edge of the cube-shaped primitive vertebra. As the upper edges of two opposing arches grow together over the medullary tube from right and left, the vertebral arch becomes closed.

The whole of the secondary vertebrae, which is thus formed from the union of the dorsal process of two proterosphenial pieces

and enclose a part of the embryo in its body, consists at first of a rather soft mass of cells; this afterwards passes into a firmer, cartilaginous stage, and finally into a third, permanent, bony stage. These three stages can generally be distinguished in the greater part of the skeleton of the higher vertebrates; at first most parts of the skeleton are soft, tender, and membranous, they then become cartilaginous in the course of their development, and finally bone.

At the head part of the embryo in the amnion there is usually a cleavage of the middle germinal layer into pre-ventral and lateral plates, but the dorsal and ventral somites are isolated from the first, and form what are called the "head-plates" (fig. 142 & 1). From these are

that is, the former no less than the latter the skull was originally formed from the suture-lines of a number of (at least nine) bone-servites.

While the articulation of the vertebrate body is always obvious in the eposome or dorsal body, and is clearly expressed in the segmentation of the myoseptal plates and cartilage, it is more latent in the hyposeptal or ventral body. Nevertheless, the hyposeptalities of the vegetal half of the body are not less important than the aposeptalities of the animal half. The segmentation of the ventral cavity affects the following principal systems of organs : 1. the gonads or sex-glands (gastroneuræ); 2. the neurenteric or kidney (neuro-uræ).



That, and the—What do you think, of  
the Ward day? We took them to the French. They are  
so hospitable. And we had a delicious dinner there.  
The English were excellent, too. I am so glad we  
had a good time. I am so glad we had a good time.

formed the skull, the body, base of the brain, and the muscles and bones of the body. The skull develops as the same way as the membranous vertebral column. The right and left halves of the head curve over the cerebral vesicle, enclose the foremost part of the chords below, and thus finally form a smooth, soft, membranous capsule about the brain. This is afterwards converted into a cartilaginous primitive skull, such as we find permanently in many of the fishes. Much later this cartilaginous skull becomes the permanent bony skull with its various parts. The bony skull in turn and all the other structures is more highly differentiated and modified than that of the lower vertebrates, the amphibia, and fishes. But as the one has arisen phylogenetically from the other, we must

The eye - blind or a dog's eye, more from the front, & the re-located half - not the present eye - less, & a remnant of it. It had never been able to see even of yesterday - except in pictures, & his eyes were now closed, & his head, & hands, & feet, & all his body, were now as dead as if he had been buried in a grave, & might continue a spirit of the earth, with those eyes of darkness, which go to the judgment. (From  
Ghosts.)

towed); and 3, the hand-gut with its relatives (hemp-shoots).

The segmentation of the hypodermis is low, conspicuous because in all the craniotes the cavities of the ventral segments, to the walls of which the sexual products are developed, have long since coalesced, and formed a single large body-cavity, owing to the disappearance of the partitions. This catagenetic process is so old that the cavity seems to be unsegmented from the first in all the craniotes, and the rudiment of the gonads also is almost always unsegmented. It is the more interesting to learn that, according to the important discovery of Ruckert, this sexual structure is at first segmented even in the animal vertebrates, and the several

gonotomes only bleed into a single second gland on either side laterally.

*Amphioxus*, the sole surviving representative of the ascidians, once more yields us most interesting information; in this case the sexual glands receive no segmental

cavities, formed from the hyposomites of the fresh.

The glands are the most important segmental organs of the hyposoma, in the sense that they are phylogenetically the oldest. We find sexual glands (as pouch-

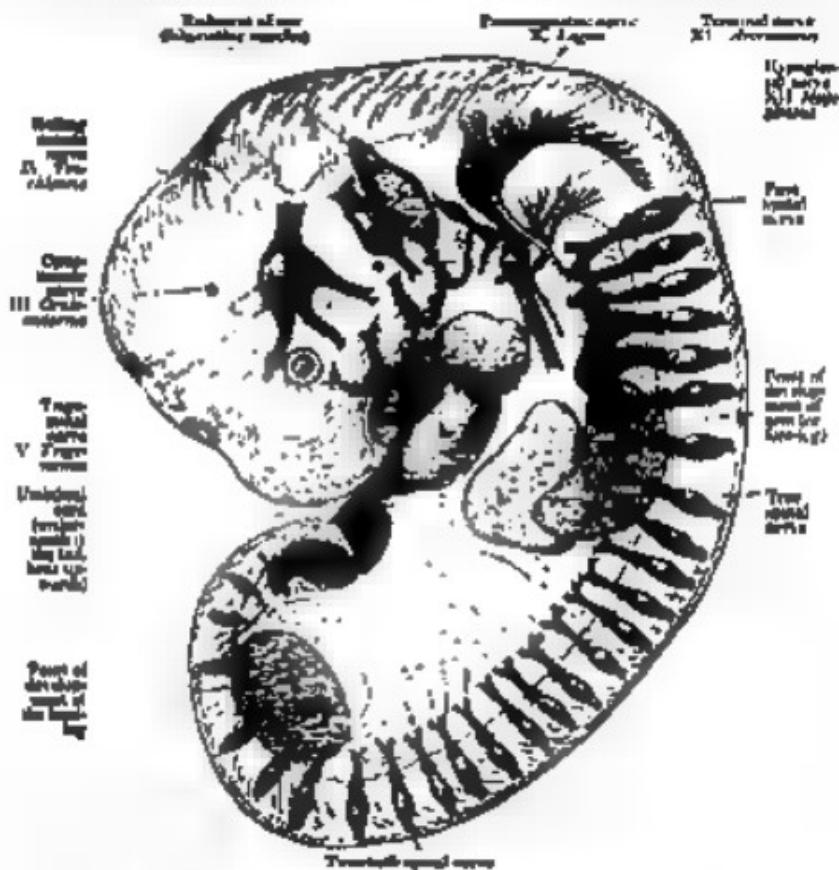


FIG. 30.—Nervous system of the frog's rectal ganglion. Stage 30, magn. 600. See figs. 30, 31. The segments of the cerebral commissum and the roots of the spinal nerves are separately marked. Underneath the first ganglion (at right) is the lower (posterior) V. and W. trunk; A., under the second, the lower T. & P.

throughout life. The sexually mature lancelet has, on the right and left of the gut, a series of metanephridial sacs, which are filled with ova in the female and sperm in the male. These segmental gonads are originally nothing more than the real gonadomes, separate body-

appendages of the gastro-caecal system; in most of the lower animals, even in the cyclostomes, etc., which have no kidneys. The latter appear first (as a pair of excretory tubes) in the pleopodes (annelids), and have probably been inherited from these by the articulates.

(anomolids) on the one hand and the unsegmented proctodaeum on the other, and from these passed to the articulated vertebrates. The oldest form of the kidney system in this stem are the segmental pronephridia or protonephridia, in the same arrangement as Bewarji found them in the amphioxus. They are small canals that lie in the frontal plane, on each side of the dura, between the epiphysis and hypophysis (Fig. 160a), their internal funnel-shaped opening leads into the various body-cavities; their outer opening is the lateral furrow of the epidermis. Originally they must have had a double function, the carrying away of the urine from the spermatheca and the release of the sexual cells from the hypophysis.

The recent investigations of Rudert and Van Wyhe on the mesoblastic segments of the trunk and the excretory system of the salamander show that these "primitive statoblasts" are closely related to the nephridia in this further respect. The transverse section of the chick-embryo in Fig. 161 shows this very clearly.

In other higher vertebrates, also, the kidneys develop (though very differently formed later on) from coelomic structures, which have been secondarily derived from the segmental pronephridia of the arachnid. The parts of the mesoderm at which the first traces of them are found are usually called the middle or metanephric plates. As the first traces of the gonads make their appearance in the middle plates nearer toward (or middle) from the inter-furrows of the nephro-ovaria, it is better to count the part of the mesoderm with the hypophysis.

The chief and oldest organ of the vertebrate hypophysis, the alimentary canal, is generally described as an unsegmented organ. But we could just as well say that it is the oldest of all the segmented organs of the vertebrates; the double row of the coelom-pouches grows out of the dorsal wall of the gut, on either side of the dura. In the brief period when segmental coelom-pouches are still openly connected with the gut, they look just like a double chain of segmented visceral glands. But apart from this, we have originally in all vertebrates an important articulation of the fore-gut, that is wanting in the lower gut, the

gut, and the gill-arches that separated them, were presumably also segmental, and distributed among the various restorations of the chain, like the gonads in the after-gut and the nephridia. In the amphioxus, too, they are still segmentally formed. Probably there was a division of labour of the hyponephridia in the older (and long extinct) arachnids, in such wise that those of the fore-gut took over the function of insulating and those of the after-gut that of reproduction. The former developed into gall-pouches, the latter into



Transverse section of the chick-embryo showing the early development of the excretory system.

mid-coelom. The gut, however, has a

two-pairing. There may have been primitive kidneys in both. Though the gills have lost their function in the higher vertebrates, parts of them have been gradually maintained in the embryo by a transverse heredity. At a very early stage we notice in the embryo of man and the other amniotes, at each side of the head, the remarkable and important structures which we call the gill-arches and gill-clefts (Figs. 167-170 f.). They are the characteristic and invariable organs of the amniote-embryo, and are found always in the same

The gill-clefts, which originally in the older arachnids placed the wall of the fore-

spot and with the same arrangement and structure. There are formed to the right and left in the lateral wall of the fore-gut cavity, in its foremost part, first a pair and then several pairs of meatus-shaped inlets, that pierce the whole thickness of the lateral wall of the head. They are thus converted into shelves, through which one can penetrate freely from without into the gutlet. The wall thickness between these branchial folds, and changes into an arch-like or meatus-shaped past—the gill, or gutlet-arch. In this the muscles and skeletal parts of the head

higher vertebrates they afterwards disappear. The branchial arches are converted partly into the jaws, partly into the bones of the tongue and the ear. From the first gill-cleft is formed the tympanic cavity of the ear.

There are few parts of the vertebrate organism that, like the outer covering or integument of the body, are not subject to metamorphosis. The outer skin (*epidermis*) is unsegmented from the first, and proceeds from the continuous horny plate. Moreover, the underlying cuts are also not segmental, although it develops from the segmental structure of the cut-plate (Figs. 162, 163). The vertebrates are strikingly and profoundly different from the annelids in these respects also.

Further, most of the vertebrates will have a number of unsegmented organs, which have arisen locally, by adaptation of particular parts of the body to certain special functions. Of this character are the unsegmented in the spinal, and the brain, the heart, the spleen, and the large ventral glands—lungs, liver, pituitary, etc.—in the hyposoma. The heart is originally only a broad spindle-shaped enlargement of the large ventral blood-vessel or principal vein, at the point where the unsegmented passes into the branchial artery, at the base of the head and trunk (Figs. 170, 172). The three higher sense-organs—nose, eye, and ear—were originally developed in the mid-fossa in all the classes, as three pairs of small depressions in the skin at the sole of the head.

The organ of smell, the nose, has the appearance of a pair of small pits above the mouth-pit, in front of the head (Fig. 181 a). The organ of sight, the eye, is found at the side of the head, also in the shape of a depression (Figs. 169 f, 170 d), to which corresponds a large outgrowth of the foremost cerebral vesicle on each side. Farther behind, at each side of the head, there is a third depression, the first trace of the organ of hearing (Fig. 169 g). As yet we can see nothing of the later elaborate structure of these organs, nor of the characteristic build of the face.

When the human embryo has reached



FIG. 171.—Diagrammatic section of the young embryo, and head-lgs of a chick-bird, at the time of migration after birth. A, nostril; B, optic vesicle; C, brain; D, eye; E, ear; F, heart; G, liver; H, pituitary; I, gills; J, mouth; K, nostril; L, eye; M, ear; N, heart; O, liver; P, pituitary; Q, gills; R, mouth; S, nostril; T, eye; U, ear; V, heart; W, liver; X, pituitary; Y, gills; Z, mouth. (From H. Müller.)

got separated; a blood-vessel with rings afterwards on their inner side (Fig. 169 d). The number of the branchial arches and the clefts that alternate with them is four or five on each side in the higher vertebrates (Fig. 170 d, f, i, s, f'). To some of the fishes (teleostei) and in the cyclostomes we find six or seven of them permanently.

These remarkable structures had originally the function of respiratory organs—gills. In the fishes the water then serves for breathing, and is taken near the mouth, will always pass out by the branchial clefts at the sides of the gutlet. In the

... stage of development, it can still scarcely be distinguished from any other higher vertebrate. All the chief parts of the body are now laid down: the head with

skull, the rudiments of the three higher sense-organs and the five cerebral vesicles, and the gill-arches and chorda, the trunk

significantly. From it we can gather the most important phylogenetic conclusion.

There is still no trace of the limbs. Although head and trunk are separated and all the principal internal organs are laid down, there is no indication whatever of the "extremities" at this stage; they are formed later on. Here again we



FIG. 154.—Development of the lizard's body (Zonosaurus laticaudatus), viewed oblique to the headwards. (a, p. 3.) (b, 5.) (c, 14 days) (d, 15 days) (e, 16 days) (f, 17 days) (g, 18 days) (h, 19 days) (i, 20 days) (j, 21 days) (k, 22 days) (l, 23 days) (m, 24 days) (n, 25 days) (o, 26 days) (p, 27 days) (q, 28 days) (r, 29 days) (s, 30 days) (t, 31 days) (u, 32 days) (v, 33 days) (w, 34 days) (x, 35 days) (y, 36 days) (z, 37 days). (From V. M. Goldfarb.)

with the spinal cord, the rudiment of the vertebral column, the chain of metameres, the heart and chief blood-vessels, and the kidneys. At this stage man is a higher vertebrate, but shows no essential morphological difference from the embryos of the mammals, the birds, the reptiles, etc. This is an ontogenetic fact of the greatest

interest. It is evident that the older vertebrates had no limbs, and it must be the case in the lowest vertebrates (amphioxus and the lancelets). The descendants of these primitive vertebrates only acquired limbs—two fore-limbs and two hind-limbs at a much later stage of development.

at first all alike, though afterwards very considerably in structure—becoming fine (of bone and belly) in the fishes, wings and legs in the birds, fore and hind legs in the creeping

which represent at first simple rounded knobs or plates. Gradually each of these plates becomes a large projection, in which we can distinguish a small inner part and a broader outer part. The latter



FIG. 172.—*Rana esculenta*, five weeks old, last 12 hind legs, worn from the right, magnified two times (From Frost's *Practical Anatomy and Histology*). In the undivided limb we see the eye, nostril, and ear. In the limb the skin and part of the muscles have been removed, so that the cartilaginous ventral column is free; the dorsal root of a spinal nerve gives out from each vertebra (except the one at the base). In the middle of the lower half of the figure part of the chin and sternocleidomastoid muscle are visible. The skin and muscles have also been removed from the right limb; the undivided remnants of the five fingers of the limb, and five rays of the foot, are clearly seen; under the dermal plate, and often the strong network of nerves that goes from the spinal cord to the extensors. The tail projects under the skin, and to the right of it is the first part of the umbilical

animal, arms and legs in the apes and man. All these parts develop from the same simple original structure, which forms secondarily from the transverse wall (Figs. 172, 173). They have always the appearance of two pairs of small buds,

in the rudiment of the foot or hand, the former that of the leg or arm. The similarity of the original rudiment of the limbs in different groups of vertebrates is very striking.

How the few fingers or toes with their

Blood-vessels gradually differentiate within the simple fin-like structure of the limb in the embryo of the lizard in Fig. 174. They are formed at just the same way in man, in the human embryo of five weeks the five fingers can clearly be distinguished within the fin-plate (Fig. 175).

The careful study and comparison of

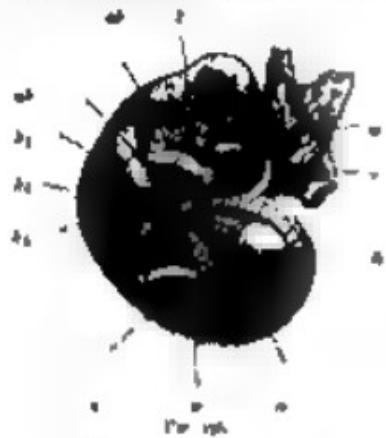


FIG. 174.



FIG. 175.

Human embryo with those of other vertebrates in the stage of development is very instructive, and reveals more mysteries to the impartial student than all the religions in the world put together. For instance, if we compare attentively the three successive stages of development that are represented, in twenty different animals we find a remarkable likeness. When we see that as a fact

twenty different animals of such divergent characters develop from the same embryonic form, we can easily understand that they may all descend from a common ancestor.

In the first stage of development, in which the head with the five cerebral vesicles is already clearly indicated, but there are no limbs, the embryos of all the vertebrates, from the fish to man, are only incidentally or not at all different from each other. In the second stage, which follows the first, we begin to see differences between the embryos of the lower and higher vertebrates; but the human



FIG. 176.

FIGS. 174-176.—Embryos of the bat (*Myotis*) compared at three different stages. From Oskar Hertwig. Fig. 174. Radiolarian larva in a feeding & breathing & teleostean depression, a, olfactory pit; b, epibranchial groove; c, liver; d, gills; e, heart; f, gut; g, foregut; h, liver; i, epibranchial groove; j, mouth; k, eye; l, brain; m, spinal cord; n, heart; o, gut; p, liver; q, foregut; r, epibranchial groove; s, mouth; t, eye; u, brain; v, spinal cord; w, heart; x, gut; y, liver; z, foregut. FIG. 175. Radiolarian of later metazoan development still between fin and hind-leg = forelimb could a cross-section of living mammals. FIG. 176. The finer membranes developed and are being thrown over fingers of the hands, which cover the face.

embryo is still hardly distinguishable from that of the higher mammals. In the third stage, in which the gall-nerves have disappeared and the face is formed, the differences become more pronounced. These are facts of a significance that cannot be exaggerated.<sup>1</sup>

<sup>1</sup> Because they also form the most diverse structures may be developed from a common form. As we actually see them at the time of the review on, we have a right to assume it is that of the stem-form. Nevertheless, the resemblance, however great, is never a real identity. Even the members of the different sub-orders of our species are really not really identical. If the reader would consult the complete edition of that work at a library, he will find not plates illustrating these twenty embryos.

If there is an intimate causal connection between the processes of embryology and stem-history, as the result seems to indicate of the laws of heredity, several important phylogenetic conclusions follow at once from these ontogenetic facts. The profound and remarkable similarity in the embryonic development of man and the

other vertebrates can only be explained when we admit their descent from a common ancestor. As a fact, this common descent is now accepted by all competent scientists; they have substituted the material evolution for the supernatural creation of organisms.

## CHAPTER XV.

### FETAL MEMBRANES AND CIRCULATION

AMONG the many interesting phenomena that we have encountered in the course of human embryology, there is an especially

the other placental mammals. As a fact, all the eutherian mammals that draw up the mammals from other



FIG. 17.—Specimens obtained from the second to the fifteenth week, natural size, seen from the left. The right hand turned toward the right. (Courtesy from *Schäfer's Lehrbuch der Anatomie des Menschen*, Vol. II of *Lehrbuch der Anatomie des Menschen*, VIII of *Lehrbuch der Anatomie des Menschen*, XI of *Lehrbuch der Anatomie des Menschen*, XV of *Lehrbuch der Anatomie des Menschen*.)

importance in the fact that the development of the human body follows from the beginning just the same law as that of

animals are found also in man; even the ovary with its distinctive membranes (ova folliculae, Fig. 14) shows the same typical

structure in all mammals (except from the older oviparous monotremes). It is long since been deduced from the structure of the developed man that his man's place in the animal kingdom is among the mammals. Linnaeus (1758) placed him

with the apes, as one and the same order (*Primates*), in his *Système Natura*. This position is fully confirmed by comparative embryology. We see that man entirely resembles the higher mammals, and most of all the apes, in embryonic development as well as in anatomical structure. And if we seek to understand this ontogenetic agreement in the light of the biogenetic law, we find that it proves clearly and necessarily the descent of man from a series of other mammals, and predominantly from the primates. The common origin of man and the other mammals from a single ancient stem-form can no longer be questioned, nor can the immediate blood-relationship of man and the ape.

The essential agreement in the whole bodily form and inner structure is still seen in the embryo of man and the other mammals at the low stage of development at which the mammal-body can be recognized as such. But at a somewhat earlier stage, in which the limbs, gillarches, sense-organs, etc., are already outlined, we cannot yet recognize the mammal embryo as such, or distinguish them from those

you consider still earlier stages of development, were unable to discover any essential difference in bodily structure between the embryos of these higher vertebrates and those of the lower, the amphibia and fishes. If, in fine, we go back to the construction of the body out of the four germinal layers, we are astonished to perceive that these four layers are the same in all vertebrates and everywhere take a similar part in the building-up of the fundamental organs of the body. If we compare as to the nature of these four secondary layers, we know that they always arise in the same way from the two primary layers; and the latter have the same significance in all the metazoa (i.e., all animals except the

monadines). Finally, we see that the cells which make up the primary germinal layers owe their origin in every case to the repeated cleavage of a single simple cell, the stem-cell or fertilized ovule.

It is impossible to lay too much stress on this remarkable agreement in the chief embryonic features in man and the other animals. We shall make use of it later on for our monophyletic theory of descent—the hypothesis of a common descent of man and all the metazoa from the gamete. The first rudiments of the principal parts



The diagram shows three embryos of the fourth week, sections of an adult whale (1), from the womb of a female cow (2), and of a dog (3). The embryo of the whale (1) is the largest, and the dog (3) the smallest. The embryo of the cow (2) is intermediate. The numbers refer to the numbered points in the text for the various parts.

of the body, especially the oldest organs, the alimentary canal, are the same everywhere, they have always the same extremely simple form. All the peculiarities that distinguish the various groups of animals from each other only appear gradually in the course of embryonic development; and the closer the relation of the various groups, the later they are found. We may formulate this as follows:

As a rule, the more remote the group, the more it can be regarded as an appendix to our biogenetic law. This is the law of a ontogenetic connection of related animal forms. It runs: The closer the

relation of two fully-developed animals in respect of their whole body structure, and the nearer they are connected in the classification of the animal kingdom, the longer do their embryonic forms retain their identity, and the longer is it impossible (or only possible on the ground of subordinate features) to distinguish between their embryos. This law applies to all animals whose embryonic development is, in the main, an hereditary summary of their ancestral history, or in which the original form of development has been faithfully preserved by heredity. When, on the other hand, it has been altered by congenital, or disturbance

characteristic formation of its membrane (*zona pellucida*), which clearly distinguishes it from the ovum of all other animals. When the human fetus has attained the age of fourteen days, it forms a small vesicle (or "embryonic vesicle") about a quarter of an inch in diameter. A thicker part of its border forms a simple saucer-shaped embryonic shield one-twelfth of an inch long (Fig. 13). On its dorsal side we find at the middle line the straight mid-gut fissure, bordered by the two parallel dorsal or medullary swellings. Behind, it passes by the neurenteric canal into the primitive gut or primitive gut-tube. From this the folding of the two ectodermic processes in the same way as in the other mammals (cf. Fig. 14, p. 97). In the middle of the saucer-shaped embryonic shield the first primitive segment immediately begins to make their appearance. At this age the human embryo cannot be distinguished from that of other mammals, such as the hare or dog.

Later (or after the twentieth day) the human embryo has doubled its length; it is fifth of an inch



FIG. 13.—Dorsal aspect of the vesicle of the 14th day, measured at its mid-long. (From Prof. J. L. Jackson's 'Fig. 13, except of course of skull, at upper part, & recto-umbilical

of development, we find a limitation of the law, which increases in proportion to the introduction of new features by adaptation (cf. Chapter I., pp. 4-6). That the apparent exceptions to the law can always be traced to congenital.

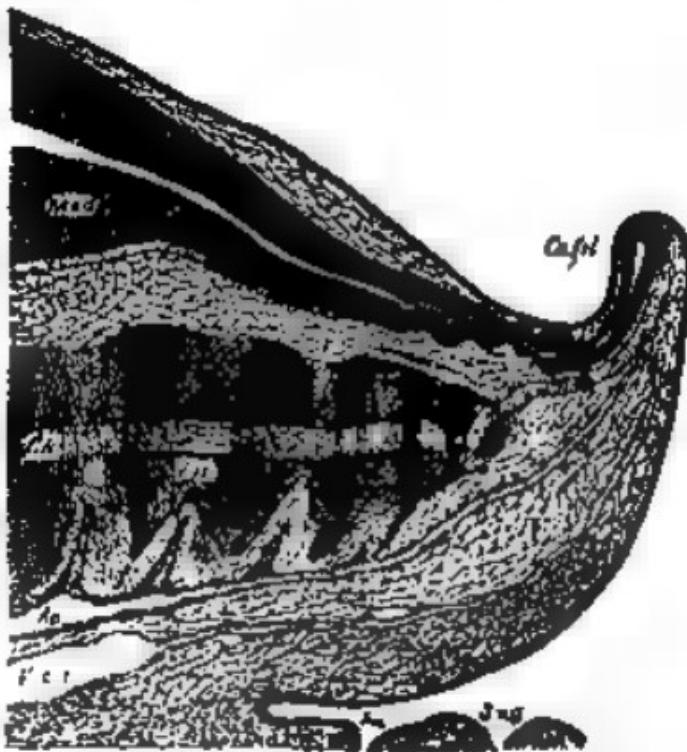
When we apply to man this law of the congenital connection of related forms, and run rapidly over the earliest stages of human development with an eye to it, we notice first of all the structural identity of the ovum in man and the other mammals at the very beginning (Figs. 1, 14). The human ovum possesses all the distinctive features of the ovum of the viviparous mammals, especially the

the three major nerve-organs, and the rudiments of the gall-bladder, which pierce the wall of the neck (Fig. 14, III.). The alimentary tract given out of the gut behind. The embryo is already entirely enclosed in the amniotic fluid, and is only connected in the middle of the belly by the vitelline duct with the embryonic vesicle, which changes into the yolk-sac. There are no extremitas or limbs at this stage, no trace of arms or legs. The head-end has been strongly differentiated from the tail-end, and the first outlines of the cerebral vesicles are fr. below, under the fore-brain or less, clearly we see the nose. There is at this stage a special character that distinguishes the human embryo from those of other mammals.

A week later (after the fourth week, i.e. the twenty-eighth to thirtieth day of development) the human embryo h-

reached a length of about one-third of an inch (Fig. 179, IV). We can now clearly distinguish the head with its various parts, inside it the five primitive cerebral vesicles (fore-brain, middle-brain, intermediate-brain, hind-brain, and after-brain); under the head the gill-slits, which divide the gill-clefts; at the sides of the head the rudiments of the eyes, a couple of pits in the outer skin, with a

hand-bend over the trunk, almost at a right angle. The latter is still connected in the midline of its ventral side with the amniotic vesicle; but the embryo has still further severed itself from it, so that it already hangs out as the yolk-sac. The hind part of the body is also very much curved, so that the pointed tail-end is directed towards the head. The head and face-part are made entirely on the



MEDIAN LONGITUDINAL SECTION OF THE TAIL OF A HUMAN EMBRYO, TWO-THIRDS OF AN HOUR LONG.  
[From *Atlas der Entwicklung*; Prof. Max Brügel's collection.] *Cat.* of central nervous system, or spinal cord, or spinal meninges, 1900.

pair of corresponding simple vesicles growing out of the lateral wall of the fore-brain (Figs. 180, 181 a). Far behind the eyes, over the last gill-clefts, we see the vesicular rudiment of the respiratory organ. The rudimentary limbs are now clearly outlined—four simple buds of the shape of round plates, a pair of fore (fg.) and a pair of hind legs (hg.), the former a little larger than the latter. The large

hind bend over the trunk, almost at a right angle. The latter is still connected in the midline of its ventral side with the amniotic vesicle; but the embryo has still further severed itself from it, so that it already hangs out as the yolk-sac. The hind part of the body is also very much curved, so that the pointed tail-end is directed towards the head. The head and face-part are made entirely on the

the higher classes of vertebrates (the amniotes); it is much slimmer, or not found at all, in the lower vertebrates. At this age (four weeks) man has a considerable tail, twice as long as his legs. A vertical longitudinal section through the middle plane of this tail (Fig. 112) shows that the hinder end of the spinal marrow extends to the point M in the tail.

or *anterior sacral sinuses*, *An.*), and the principal two (*ventral sacralis* or *sacral rectum*). Underneath is the opening of the mesentery (*meso*) and the urogenital sinus (*U.G.S.*). From this anatomic structure of the human tail it is perfectly clear that



as also does the underlying chevron ('c'). The terminal continuation of the vertebral column. Of the latter, the rudiments of  
oxygenal (or lowest) vertebrae are visible—thirty-two indicate the third

and thirty-six the seventh of these. Under several columns we see the hindmost ends of the two large blood-vessels of the tail, the principal artery *furca*, consider-

The skin - mammae tubercles, two weeks old, spread over the ventral side (in Fig. 17), breast and belly-wall and liver are exposed. A wider dorsal process of upper jaw, a broad jaw, a longue, a right, left, ventralis of buccal, of left branch, a origin of aorta, R. & L. 2<sup>nd</sup> best, second, and third aorta-arches, A. C. C. were seen, as lungs (pulmonary artery), a sinusoid, in primitive kidneys (left situated), a cecum, a right middle artery, a umbilical artery, a fundus, a vesicle duct, a rectum, a tail, a shadow of heart. (From Gauth.)

It is the radiance of an apostle, the last  
boundary zone of a long h  
headed down to

private collectors to the present day.

Surgeon-General Bernhard Oerstlein, of Greece, these tailed men are not uncommon; it is not impossible that they gave rise to the ancient fables of the satyrs. A great number of such cases are given by Max Bartels in his essay on "Tailed Men" (1884, in the *Archiv für Anthropologie*, Band XV), and critically examined. These atavistic human tails are often mobile; sometimes they contain only muscle and fat, sometimes

this is involuntary in certain isolated tribes (especially in south-eastern Asia), and the

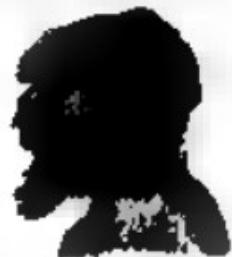


Fig. 400  
A Tailed Man.



Fig. 401.—Illustration of *Primate* in thirteen days (?) (From Albin Thomsen); a dark excrescence, divided into two parts, is covered over and concealed. Within the outer division the tiny curved fingers lie on the large vascular veins to the left above.

rudiments of caudal vertebrates. They attain a length of eight to ten inches and more. Graysville Harrison has very carefully studied one of those cases of "pig-tail," which he removed by operation from a six months' old child in 1850. This tail moved briskly when the child cried or was excited, and was drawn up when at rest.

In the opinion of some travellers and anthropologists, the strobilic tail-forma-



Fig. 402

Fig. 402.—Illustration of the same. (From Albin Thomsen); a dark, oval, excrescence, the small finger is the right hand above.

Fig. 403.—Illustration of the same, taken from the preceding figure, magnified ten times, & showing that the vascular groove already closed, & had



Fig. 403



Fig. 404.—Illustration of *Primate* in twenty to twenty-four days (From Albin Thomsen); Natural size, magnified ten times, shows a dark, oval, excrescence, the small finger is the right hand to the right above.



Fig. 405.—Illustration from the preceding figure, magnified ten times, & showing a late-stage process of the first development of vascular groove of skin, a small skin fold with fine wrinkles near below. Three gold-disks are placed near the umbilical furrowing, & auxiliary vessels, &c., are visible.

archipelago), so that we might speak of a special race or "species" of tailed men.

(Howe, *see below*). Bartels has "seen; large, and almost fills the whole of the abdominal cavity, and is surrounded by a thin membrane which is very delicate, and easily torn." (Fig. 183 ev). Behind it are the rudimentary lungs. The primitive kidneys (*see below*) are very large, they fill the greater part of the abdominal cavity, and extend from the liver (*ibid.*) to



FIG. 183.—Human embryo of sixteen to eighteen days. (From Oster.) Magnified. The embryo is surrounded by the amnion (*ibid.*) and lies within the expanded yolk-sac vesicle. The latter is drawn up by the large yolk-sac of the hindgut to the inner wall of the allantois, overlaid by the short and thick peritoneal fold. Shows the normal convex curve of the body after each a long, elongated oval or elongated concave surface, & hence, in parallel strobiles. The spots on the outer wall of the membranes are the tufts of the branching chorionic villi which are free at the border.

month (Fig. 183), we find the alimentary canal formed in the body-cavity, and for the most part cut off from the embryonic vesicle. There are but mouth and anus apertures. But the mouth-cavity is not yet separated from the nasal cavity, and the face not yet shaped. The heart shows all its four sections, it is very

short month all the chief organs are already outlined. But there are at this stage no features by which the human embryo materially differs from that of the dog, the hare, the ox, or the horse—in a word, of any other higher animal. All these embryos have the heart, or at least a very similar, heart; they can at the most be

distinguished from the human embryo by the total size of the body or some other insignificant difference in size. Thus, for instance, in man the head is larger in proportion to the trunk than in the dog.

The features, by means of which we distinguish between them are not clear until later on. Even at a much more advanced stage of development, when we can distinguish the human fetus from that of

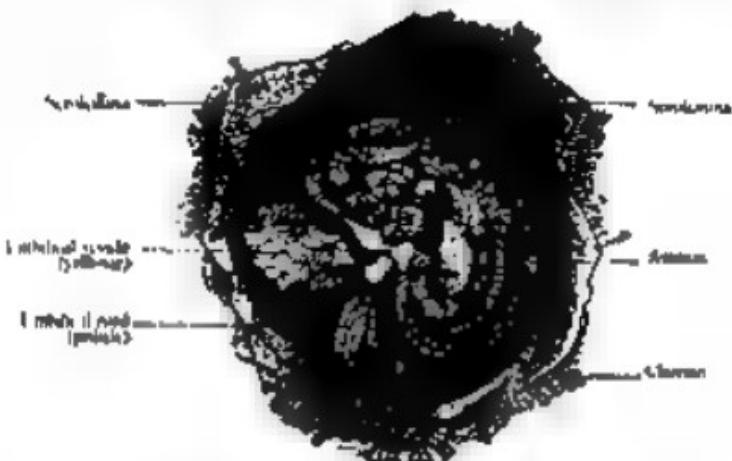


FIG. 170.—Histological section of the fourth week embryo of an adult dog. *Inset* = the dissected chorion.

the tail is rather longer in the dog than in man. There are no recognizable differences. On the other hand, the whole internal organization and the form and arrangement of the various organs are essentially the same in the human embryo at four weeks as in the embryos of the other mammals at corresponding stages.

It is otherwise in the second month of human development. Fig. 170 represents a human embryo of six weeks (VI), one of seven weeks (VII), and one of eight weeks (VIII), at natural size. The differences which mark off the human embryo from that of the dog and the lower mammals now begin to be more pronounced. We can see important differences at the sixth, and still more at the eighth, week, especially in the formation of the head. The size of the various sections of the brain is greater in man, and the tail is shorter. Other differences between man and the lower mammals are found in the relative size of the internal



of the closely related mammals—the... especially the anthropoid apes,

in appearance at a glance. A still closely resembles them... but we get the distinctive features, and

we can distinguish the human embryo confidently at the first glance from that of all other mammals during the last four months of fetal life—from the sixth to the ninth month of pregnancy. Then we begin to find also the differences between the various races of men, especially in regard to the formation of the skull and the face. (Of Chapter XXXII.)

The striking resemblance that persists so long between the embryo of man and of the higher apes disappears much earlier in the lower apes. It naturally remains

famous Miss Julia Puttrana, Fig. 185). It will be admitted to represent a higher stage of development. There are still people among us who look especially to the face for the "image of God in man." The long-nosed ape would have more claim to this than some of the stumpy-nosed human individuals one meets.

This progressive divergence of the human from the animal form, which is based on the law of the ontogenetic connection between related forms, is found in the structure of the external organs as well



FIG. 190.—*Macacus fasciatus* with the nose broken, six weeks old. The outer envelope of the skin, even at this advanced, usually external, state is breaking up, a symptom of the nervous insufficiency. The embryo, a monkey, is its delicate environment. The pathos is increased in a small primate much more rapidly than in the large simians. In the latter, indeed, the reflex death in the womb sooner kills off the abortion the inner tissues of which then gradually degenerate & form a large placenta, while the outer tissues are attached to the outer wall of the womb probably just, as from the placenta there. (Half diagrammatic.)

longest in the large anthropomorphic apes (gorilla, chimpanzee, orang, and gibbon). The physiognomic similarity of these animals, which we find so great in their earlier years, lessens with the increase of age. On the other hand, it remains throughout life in the remarkable long-nosed ape of Borneo (*Nasalis larvatus*). Its snail-shaped nose would be regarded with awe by many a man who has too little of that organ. If we compare the face of the long-nosed ape with that of abnormally ape-like human beings (such as the

as in external form. It is also expressed in the construction of the envelope and appendages that we find surrounding the fetus externally, and that we will now consider more closely. Two of these appendages—the amnion and the allantois—are only found in the three higher classes of vertebrates, while the third, the yolk-sac, is found in most of the vertebrates. This is a circumstance of great importance, and it gives us valuable data for constructing man's genealogical tree.

As regards the external membrane that encloses the eggs in the mammal womb,

we find it just the same in man as in the higher mammals. The embryo, the reader will remember, first surrounded by the transparent structureless ectolemma or amniotic fluid (Figs. 1, 14). But very soon, even in the first week of development, this is replaced by the permanent chorion. This is formed from the external layer of the tunica, the amniotica, or "inner membrane," the formation of which we shall consider presently; it surrounds the fetus and its appendages as a broad, completely-closed sac; the space between the two, filled with clear watery fluid, is the amniotic, or water-tight cavity.

As one-third of an inch in diameter (Figs. 216-219), as a large quantity of fluid gathers inside it, the chorion expands more and more, so that the embryo only occupies a small part of the space within the vesicle. The villi of the chorion grow larger and more numerous. They branch out more and more. At first the villi cover the whole surface, but they afterwards disappear from the greater part of it, they then develop with proportionately greater vigour at a spot where the placenta is formed from the allantois.

When we open the chorion of a human embryo of three weeks, we find on the

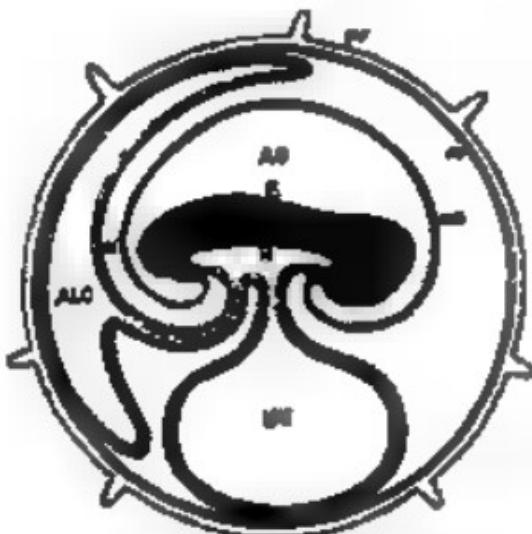


FIG. 214.—Stages of the embryonic organs of the simplest chord mammals and mammals (From Tschirhart's "C. H. W. Beck's, publisher, and later given Name of the embryonic chick," *Arch. of Anatomy* 1916, 1921-1922).

("extra-embryonic body-cavity"). The smooth surface of the sac is quickly covered with numbers of Roy cells, which divide the like into (Fig. 192, 193, 216-219).

ponding depressions that are formed by the tubular glands of the uterine mucilage of the maternal womb. Thus, the ovum secures its permanent seat (Figs. 185-192).

In human ova of eight to twelve days, this external membrane, the chorion, is already covered with small pustules or vesicles, and forms a ball or spheroid of one-fourth

inch side of the fetus a large sac, filled with fluid. This is the yolk-sac, or "yolk-vessel," the origin of which we have considered previously. The larger the embryo becomes the smaller we find the yolk-sac. In the end we find the remains of it in the shape of a small pear-shaped vesicle, fastened by a long thin stalk (or pedicle), and hanging from the open belly of the fetus (Fig. 204). This pedicle is the vitelline duct, and is separated from the body at the closing of the navel.

Behind the yolk-sac a second appendage,

of much greater importance, as formed at an early stage at the belly of the chimaera embryo. This is the allantois or "proto-urinary sac," an important embryonic organ, only found in the three higher classes of vertebrates. In the three higher classes the allantois quickly appears at the hinder end of the alimentary canal, growing out of the cavity of the yolk-sac (Fig. 147, p. 4; Fig. 193, *etc.*)

The further development of the allantois varies considerably in the three sub-classes of the mammals. The two lower sub-classes, monotremes and marsupials, retain the simpler structure of their ancestors, the reptiles. The wall of the

the embryo which we call the placenta.

The pedicle of the allantois, which connects the embryo with the placenta, and conducts the strong umbilical vessels from the former to the latter, is covered by the amnion, and with this amniotic sac and the pedicle of the yolk-sac, forms what is called the *umbilical cord* (Fig. 196 *etc.*). As the large and blood-filled vascular network of the fetal allantois attaches itself closely to the mucous lining of the maternal womb, and the partition between the blood-vessels of mother and child becomes much thinner, we get that remarkable negative separation of the fetal body which is characteristic of the placenta (or chorion). We shall return afterwards to the closer consideration of this (cf. Chapter XXIII.)

In the various orders of mammals the placenta undergoes many modifications, and these are of great evolutionary importance and useful in classification. There is only one of these that need be specially mentioned—anthropoid apes, established by Lebedeva in 1890, that the distinctive human placenta is confined to the anthropoids. In this most advanced group of the mammals the allantois is very small, soon loses its cavity, and then, in common with the urinaria, undergoes certain peculiar changes. The umbilical cord develops in this case from what is called the "central pedicle." Until very recently this was regarded as a structure peculiar to man. We now know from Solonka, that the single-developed ventral pedicle is merely the pedicle of the allantois, combined with the pedicle of the amnion and the endometrial pedicle of the yolk-sac. It has just the same structure in the orang and gibbon (Fig. 197), and very probably in the chimpanzee and gorilla, as in man. It is, therefore, not *a character*, but a striking fresh proof, of the blood-relationship of man and the anthropoid apes.

We find only in the anthropoid apes—the gibbon and orang of Asia and the chimpanzee and gorilla of Africa—the peculiar and unique formation of the placenta that characterizes man (Fig. 198).

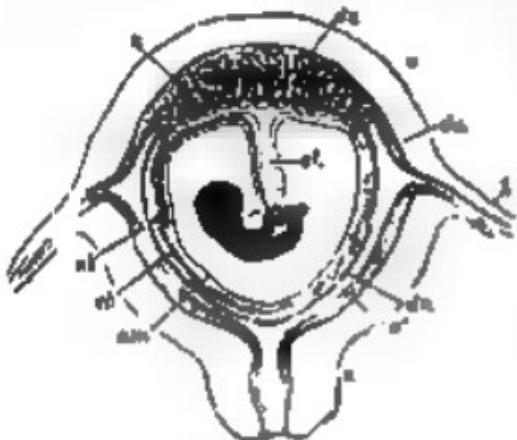


Fig. 197.—Diagrammatic frontal section of the primate fetus. *Bornean orang* (from Solonka). The arrows show by the umbilical cord which connects the pedicle of the allantois fully developed ventral pedicle of the amnion, *st.* cerebrum, *gt.* gut, *am.* amnion, *pl.* placenta, *ur.* urinaria, *y.s.* yolk-sac.

allantois and the enclosing serous sac remains smooth and without folds, as in the birds. But in the third sub-class of the mammals the serous sac forms, by imagination at its outer surface, a number of hollow tufts or villi, from which it takes the name of the chorion of Metzgerius. The gut-like layer of the allantois, richly supplied with branches of the umbilical vessel, projects into these tufts of the primary chorion, and forms the "secondary chorion." Its embryonic blood-vessels are closely correlated to the contiguous maternal blood-vessels of the chorionic walls, and thus is formed the important nutritive apparatus of

In this case there is at an early stage an intimate blending of the chorion of the embryo and the part of the mucous lining of the womb to which it attaches. The villi of the chorion with the blood-vessels they contain grow so completely into the lining of the uterus, which is rich in blood, that it becomes impossible to separate them, and they form together a sort of cake. This comes away as the "after-birth" at parturition, at the same time, the part of the mucous lining of the womb that has united inseparably with the chorion is torn away, hence it is called the decidua ("falling-away mem-

brane"),—namely, that part of the mucous lining of the womb which unites intimately with the chorion-villi of the foetal placenta. The intact or *linea decidua / interna* or *ridge*, Fig. 196 *ds*; Fig. 199 *fj*, is that part of the mucous lining of the womb which encloses the remaining surface of the womb, the smooth chorion (*chorion laeve*), in the shape of a special thin membrane. The origin of those three different deciduous membranes, in regard to which quite erroneous views (still retained in their names) formerly prevailed, is now quite clear. The external decidua was by the specially modified and subsequently



FIG. 197.—Adult embryo of the *Melanostoma erythrura* (Mystacina australis) of Suttorps. (Muscular system.) To the left the deeper region, of which only the dorsal half is given. The embryo has been taken out and the limbs folded together, so as to determine the position and form of the muscle-plates which are attached to the walls of the womb. The embryo takes its development in the womb, and this is evident in many ways.

brane"), and also the "siderostichus,"—detachable superficial serium of the haemal vein it is performed like a mere. We find a decidua of this kind in most of the higher placentals, but it is only in man and the anthropoid apes that it divides into three parts—the outer, inner, and placental decidua. The external or true decidua (Fig. 196 *ds*; Fig. 199 *gj*) is the part of the mucous lining of the womb that clothes the inner surface of the uterine cavity wherever it is not covered with the placenta. The placental or spongy decidua (*placentalis* or *serosa*, Fig. 196 *ds*; Fig. 199 *dj*) is really the placenta itself, or the maternal part of it (*placenta*

original mucous lining of the womb. The placental *decidua serosa* is that part of the preceding which is completely transformed by the ingrowth of the chorion-villi, and is used for constructing the placenta. The inner *decidua reflexa* is formed by the rise of a circular fold of the mucous lining (at the border of the uterine neck and *myometrium*), which grows over the fetus (from the amnion) to the

The peculiar anatomic features that characterize the human fetal membranes are found no just the same way in the higher

## PIETAL MEMBRANES AND CIRCULATION

spes. Until recently it was thought that the human embryo was distinguished by its peculiar construction of a solid allantois and a special ventral pedicle, and that the umbilical cord developed from them in a different way than in the other mammals. The opponents of the unwelcome "ape-theory" laid great stress on this, and thought they had at last discovered an important indication that separated man from all the other placental. But the

described the amnion has no blood-vessels at any moment of its existence. But the other two vesicles, the yolk-sac and the allantois, are equipped with large blood-vessels, and these affect the nourishment of the amniotic body. We may take the opportunity to make a few general observations on the first circulation in the embryo and its central organ, the heart. The first blood-vessel, the heart, and the first blood-tube, are formed from the

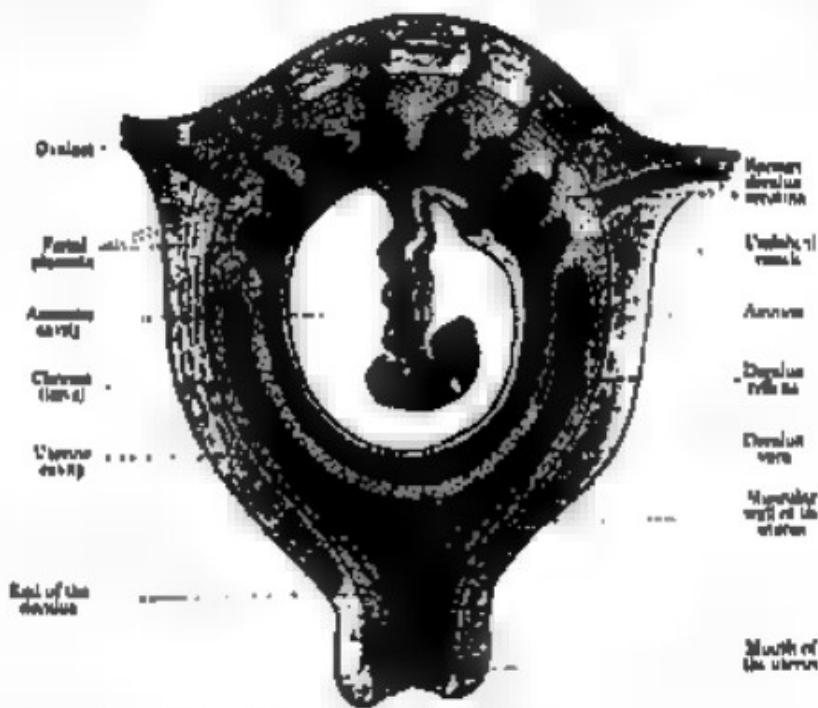


Fig. 41.—Anatomical sections of the primate embryo. <sup>27</sup>  
Diagram in the middle of the amniotic cavity, by the ventral pedicle or umbilical arteries.

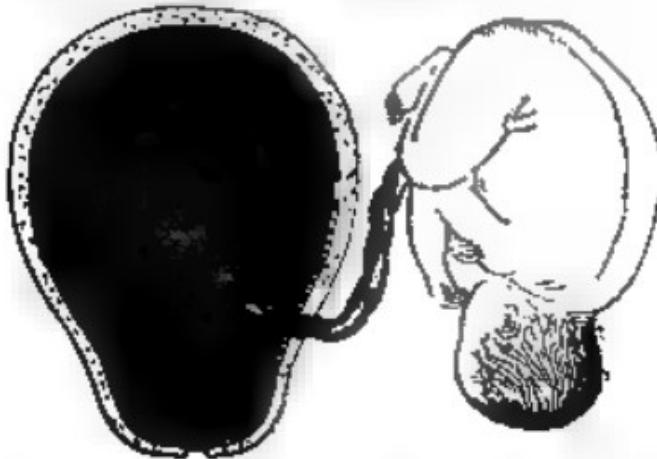
remarkable discoveries published by the distinguished zoologist Seeliger in 1890 proved that man shares these peculiarities of placentation with the anthropoid apes, though they are not found in the other apes. Thus the very feature which was advanced by our critics as a disproof became a most important piece of evidence in favour of our pithecid origin.

Of the three vesicular appendages of the amniotic embryo which we have now

met—the yolk-sac, the allantois, and the amnion—only the last is really a membrane. Hence it was called by earlier embryologists the "vascular layer." In so far the term is quite correct. But it must not be understood as if all the blood-vessels in the body came from this layer, or as if the whole of this layer were taken up only with the formation of blood-vessels. Neither of these suppositions is true. Blood-vessels may be formed independently in other parts, especially in the various products of the skin-fibre layer.



FIG. 149.—Fetal head, ventral aspect, with its membranes. Natural size. The numbers indicate from the outside to the pia mater, 1, arachnoid, 2, dura, 3, veins on meninx cerebri.



—Before birth, spaces for the air of respiration in the external portion, taken out of the membranes, the large vesicles of the lungs for the body of the fetus, in the placenta, which is connected by the umbilical cord with the fetus's heart. (From Schäfer's *Praktikum*.)

The first blood-vessels of the mammal embryo have been considered by us previously, and we shall study the development of the heart in the second volume.

In every vertebrate it lies at first in the ventral wall of the fore-gut, or in the ventral (or cardiac) mesentery, by which it is connected for a time with the wall of the body. But it soon severs itself from the place of its origin, and lies freely in a cavity—the coelom.

This lies in the wall of the fore-gut, which they enclose in a sac, and then unite above, at the upper wall of the fore-gut-cavity, to form a large single artery, that runs backward immediately under the chorda, and is called the aorta (Fig. 292 *a*). The first pair of aorta-arches lies on the lower wall of the first pair of gut-arches, and so lie between the first gut-arch (*b*) and the fore-gut (*d*), just as we find them throughout life in the

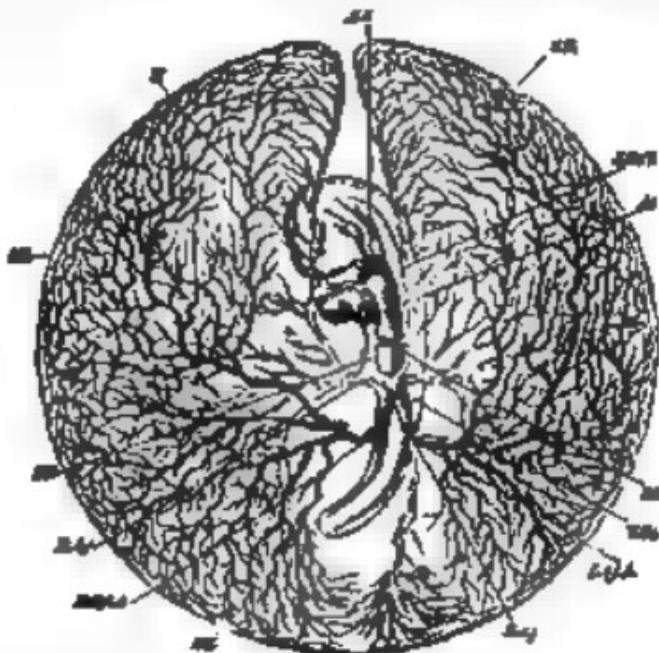


FIG. 292.—Vascular system in the gastrula stage of a chick-embryo, at the time of the third division. (From Anger.) The shaded regions represent the nervous system; the blacked parts the heart. The lines in dark, the veins light. *a*, Heart. *A*, aorta. *b*, first aorta-arches. *c*, first pair of gut-arches. *d*, second aorta-arches. *e*, gut-arches. *f*, allantois. *g*, yolk-sac. *h*, right and left aorta-arches. *i*, *j*, veins. *k*, *l*, arteries. *m*, *n*, *o*, *p*, *q*, *r*, *s*, *t*, veins and arteries. See text for full explanation.

cavity. For a short time it is still connected with the former by the thin plate of the mesocardium. Afterwards it lies quite free in the cardiac cavity, and is only directly connected with the gut-wall by the vessels which issue from it.

The fore-end of the spindle-shaped tube, which soon bends into an S-shape (Fig. 293), divides into a right and left branch. These tubes are bent upwards arch-wise, and represent the first arches of the aorta.

The single aorta, which results from the combination of these two first aortic-arches, divides again immediately into two parallel branches, which run backwards on either side of the chorda. These are the primitive aortae which we have already mentioned; they are also called the posterior vertebral arteries. These two arteries now give off at each side, behind, at right angles, four or five branches, and these pass from the embryo, body to the gastrulae-area; they

are called angioto-mesenteric or vitelline-arteries. They represent the first beginning of a fetal circulation. Thus, the first blood-vessels pass over the embryonal body and reach as far as the edge of the germinative area. At first they are limited to the dark or "vascular" zone but they,

of the embryonic vesicle. In the end, the whole of the yolk-sac is covered with a vascular net-work. These vessels

either feed the yolk-sac and convey it to the embryonic body. This is done by the veins, which pass first from the germinative area, and afterwards, from the yolk-sac, to the further end of the heart. They are called vitelline, or, frequently, angiomesenteric, veins.

These vessels naturally atrophy with the degeneration of the umbilical vesicle, and the vitelline circulation is replaced by a second, that of the allantois. Large blood-vessels are developed in the wall of the urinary sac or the allantois, as before, from the guttulae layer. These vessels grow larger and larger, and are very closely connected with the vessels that develop in the body of the embryo itself. Thus, the secondary, allantoic circulation gradually takes the place of the original vitelline circulation. When the allantois has attached itself to the inner wall of the chorion and has entered into the placenta, its blood-vessels alone effect the nourishment of the embryo. They are called umbilical vessels, and are originally double—a pair of umbilical arteries and a pair of umbilical veins. The two umbilical veins (Fig. 212 a), which convey blood from the placenta to the heart, open at first into the united vitelline veins. The latter then disappear, and the right umbilical vein goes with them, so that henceforth a single large vein, the left umbilical vein, conveys all the blood from the placenta to the heart of the embryo. The two arteries of the allantois, or the umbilical arteries (Figs. 213 a, 214 a), are merely the ultimate ramifications of the primitive aorta, which are strongly developed afterwards. This umbilical circulation is retained until the nine months of embryonic life are over, and the human embryo enters into the world as an independent individual. The umbilical cord (Fig. 196 a), in which these large blood-vessels pass from the embryo to the placenta, comes away, together with the latter, in the after-birth, and

with the loss of the lungs begins an entirely new form of circulation, which is confined to the body of the infant.

There is a great phylogenetic significance in the perfect agreement which we find between man and the anthropoid apes in these important features of embryonic circulation, and the spatial construction of the placenta and the umbilical cord. We must infer from it a close bound relationship of man and the anthropomorphic apes—a common descent of these three men and the same extinct



FIG. 212.—Specimen of placenta of the dog, from the cord side, magnified about ten times. To the right the fundus of the dog is the first pair of umbilical vessels in the foetal dog, on the right of which are the auditory vesicles. The fundus of the dog is the one which is seen.

The great number shown in Fig. 212 (the

group of lower ages). Huxley's "pith-nose-principle" applies to these ontogenetic features as much as to any other morphological relations: "The differences in construction of any part of the body are less between man and the anthropoid apes than between the latter and the lower apes."

The important Huxleyan law, the chief consequence of which is "the descent of man from the apes," has lately been confirmed in an interesting and unexpected way from the side of the experimental

physiology of the blood. The experiments of Huns Friedenthal at Berlin have shown that human blood, mixed with the blood of lower apes, has a pronounced effect on the latter, the serum destroying the blood-cells of the other. But this does not happen when human blood is mixed with that of the anthropoid ape.

As we know

that the a.

blood is only possible without injury in the case of two closely related animals as



FIG. 105.—LAP OF WHITE-BANDED gibbons (*Hylobates lar var. albimaculatus*), from the Indian mainland. (From Selenka.)

effect on the latter, the serum of the one destroys the blood-cells of the other. But this does not happen when human blood is mixed with that of the anthropoid ape.

the same family, we have another proof of the close blood-relationship, i sacred cows of the world, of man and the anthropoid ape.

The existing anthropoid apes are only a small remnant of a large family of eastern apes (or *Catarrhines*), from which man was evolved about the end of the Tertiary period. They fall into two groups

eight to twelve species of it in the East Indies. I made observations of four of them during my voyage in the East Indies (1901), and had a specimen of the orang gibbon (*Hyalobates larvatus*) living



FIG. 194.—YOUNG ORANGUTAN (*LARVATUS*).

graphical groups—the Asiatic and the African anthropoids. In each group we can distinguish two genera. The oldest of these four genera is the gibbon (*Hyalobates*, Fig. 202); there are from

four several varieties in the garden of my house in Java. I have described the interesting habits of this ape (regarded by the Malays as the wild descendant of men who had lost their way) in my *Malayan*

*Ramseleus* (chap. xi.). Psychologically, he showed a good deal of resemblance to the children of my Malay hosts, with whom I played and formed a very close friendship.

The second, larger and stronger, group of Asiatic anthropoid apes is the orang (*Pongo*), he is now found only in the islands of Borneo and Sumatra. Schreber,

lur and acent cheek-pads in the elderly male; these are wanting in the older group, the ordinary orang-outang (*Euopithecus*).

Several species have lately been distinguished in the two genera of the black African anthropoid apes (chimpanzee and gorilla). In the genus *Anthropopithecus* (or *Anthropopithecus*, formerly *Theropithecus*),



FIG. 205.—WILD ORANG (*Pongo pygmaeus*). (From R. Ardrey and Lewinsohn.)

who has published a very thorough study of the *Development and Cultural Behavior* of the *Anthropoid Ape* (1955), distinguishes ten races of the orang, which may, however, also be regarded as "local varieties or species." They fall into two sub-genera or genera, one group, *Pongo*, distinguished for the strength of its limbs, and the formation of very pro-

minent cheek-pads, the bald-headed chimpanzee, *A. trivirgatus* (Fig. 206), and the gorilla-like *A. nigripes* differ very strikingly from the ordinary *Anthropopithecus* apes (Fig. 207), not only in the size and proportion of many parts of the body, but also in the peculiar shape of the head, especially the nose and lips, and in the hair and colour. The controversy that still continues as to whether these different forms of



FIG. 56.—The banded opossum (*Aotus trivirgatus*). *Posterior view of the tail.* The vessels described by British Pathologist as "the portal veins, often considerably larger than the ordinary A. hepatis (Fig. 55) in the structure of the wall, the lumen, and the diameter of their orifice."

chimpanzee and orang are "merely local varieties" or "true species" as an idle one, as in all such disputes of classifiers there is an utter absence of clear ideas as to what a species really is.

Of the largest and most famous of all the anthropoid apes, the gorilla, Penrhyn has lately discovered a giant form in the interior of the Caucasus, which seems to differ from the ordinary species (*Gorilla*

*in that of man, but it is substantially the same. The same 300 bones, arranged in the same way, form our internal skeleton; the same 300 muscles effect our movements, the same hair covers our skin, the same groups of ganglionic cells compose the intricate mechanism of our brain; the same four-chambered heart is the central pump of our circulation." The really existing differences in the*



FIG. 209.—*Gorilla gigas* (formerly *Anthropithecus major*) (From Stoliczka.)

(Fig. 207), not only by its unusual size and strength, but also by a special formation of the skull. This giant gorilla (*Gorilla gigas*, Fig. 209) is six feet eight inches long; the span of its great arms is about nine feet; its powerful chest is twice as broad as that of a strong man.

The whole structure of this huge anthropoid ape is not merely very similar

shape and size of the various parts are explained by differences in their growth, due to adaptation to different habits of life and unequal use of the various organs. This of itself proves morphologically the descent of man from the ape. We will return to the point in the twenty-third chapter. But I wanted to point already to this important solution of "the question of questions," because that agreement

## PETAL MEMBRANES AND CIRCULATION

in the formation of the embryonic membranes and in fetal circulation which I have described affords a particularly weighty proof of it. It is the more instructive as eyes congenital structures

very in certain circumstances have a high phylogenetic value. In conjunction with the other facts, it affords a striking confirmation of our diagnostic law.



Rose flower—Petal membranes. (From Brehm.)



George Washington Carver, Negro scientist, is the founder of the Tuskegee Institute.

# THE EVOLUTION OF MAN

A POPULAR SCIENTIFIC STUDY

ERNST HAECKEL

VOL. II.

HUMAN STAMM-HISTORY, OR PHYLOGENY

TR. BY JOSEPH McCABE

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## CHAPTER XVI.

### STRUCTURE OF THE LANCELET AND THE SEA-SQUIRT

In turning from the embryology to the phylogeny of man—from the development of the individual to that of the species—

but the direct causal  
connection exists between these two

processes, which are inseparable in evolution. This important

fact finds its simplest expression in "the fundamental law of organic development," the content and purport of which we have fully considered in the first chapter. According to this biogenetic law, ontogeny is a brief and condensed recapitulation of phylogeny. If this correspondence in reproduction were complete in all cases, it would be very easy to construct the whole story of evolution on an embryonic basis. When we wanted to know the ancestors of any higher organism, and, therefore, of man—to know from what forms the race as a whole has been evolved—we should merely have to follow the series of forms in the development of the individual from the ovum; we could thus regard each of the successive forms as the representative of an ancient ancestral form. However, this direct application of ontogenetic facts to phylogenetic ideas is possible, without limitations, only in a very small section of the animal kingdom. There are, it is true, still a number of lower invertebrates (for instance, some of the Zoophytes and Vermes) in which we are justified in recognizing at once each embryonic form as the historical reproduction, or *aliquotie*, as it were, of an ancient ancestor. But in the great majority of the animals, and in the case of man, this is impossible, because the embryonic forms themselves have been modified through the change of the conditions of existence, and have lost their original character to some extent. During the immeasurable course of organic history, the many millions of years during which life was developing on our planet, success-

ive changes of the embryonic forms have taken place in most animals. The young of animals (not only deer, but also the embryo enclosed in the womb) may be modified by influence of the

time to the grandfathers of life; even species are altered during the embryonic development. Moreover, it is an advantage for all higher organisms (and the advantage is greater the more advanced they are) to shorten and simplify the original course of development, and thus to abbreviate the time of their ancestors. The higher the individual organism is in the animal kingdom, the less completely does it reproduce in its embryonic development the series of its ancestors, for reasons that are as yet only partly known to us. The fact is easily proved by comparing the different developments of higher and lower animals in any single stem.

In order to appreciate this important feature, we have distributed the embryological phenomena in two groups, *paragenetic* and *catagenetic*. Under paragenesis we count those facts of embryology that we can directly regard as a faithful synopsis of the corresponding stem-history. By ontogenesis we understand those ectoblastic processes which we cannot directly correlate with corresponding evolutionary processes, but must regard as modifications or falsifications of them. With this careful discrimination between *paragenetic* and *catagenetic* phenomena, our biogenetic law assumes the following more precise shape: rapid and brief development of the individual (ontogeny) is a condensed synopsis of the long and slow history of the stem (phylogeny); this synopsis is the identical and complete in proportion as the original features have been preserved by heredity, and modifications have not been introduced by adaptation.

In order to distinguish correctly between palaeontic and comparative plateaux in embryology, and obtain mutual assistance in connection with embryology, we must especially make a comparative study of the larvae. In doing this it is best to employ the methods that have long been used by paleontologists for the purpose of establishing the succession of the evolutionary periods on the crust of the earth. The solid crust, a thick envelope, the giving way of which gives rise to thin shells, is composed of different kinds of rocks; there are, first, the volcanic rocks which have formed directly by the cooling at the surface of the molten mass of the earth; secondly, there are the sedimentary rocks, that have been made out of the remains of water, and these have had an important share in the making of the sea. Much of these sedimentary rocks are not of the soft layer of mud, but in the course of thousands of years a concretion has a solid, hard mass of stone (sandstone, limestone, marl, &c.), and at the same time perfectly preserved all the solid and impermeable bodies that had沉没ed to fall into the soft mud. Among these bodies, which were either dissolved or left the greater proportion of them forming the soft stones, we have especially the more solid parts of the animals and plants that lived and died during the stages of the slow, slow.

From each of the evolutionary series has an characteristic fossils, the remains of the animals and plants that lived during that particular period of the earth's history. When we make a comparative study of these fossils, we can survey the whole series of such periods. All geologists are now agreed that we see the evolution, a definite but slow movement in the rocks, and that the time of these movements is very remote, even extremely so; so part of the world where we find the series of rocks in sequence, or even apparently opposite the common of these and of corresponding historical periods generally show a growth in the total evolution, caused by passing beyond the various parts. These areas of the variation of rocks that have been made at different points of the earth's surface [cf. Chapter XVIII].

We must not in this way be confounding the phylogeny of man. We must try to put together a fairly complete picture of

the series of our ancestors from the various phylogenetic fragments that we find in the different groups of the natural biography. We shall see that we are really in a position to form an approximate picture of the evolution of man and the mammals by a proper comparison of the embryology of very different animals—a picture that we could never have formed from the anatomy of the mammals alone. As a result of the above-mentioned comparative processes—those of dissolved and curtailed continuity—a long series of lesser stages have dropped out in the history and development of man and the other mammals, especially from the earliest periods, or have faded by modification. But we find these lesser stages in their original purity in the lower vertebrates and their descendants, especially in the last of all the vertebrates the lamprey or Ammodytes, we have the whole successive complexity preserved in the phylogenetic development. We also find comparison in place in the fishes, both stored between the lower and higher vertebrates, and later further right in the range of evolution in certain periods. Next to the fishes comes the amphibia, from the embryology of which we can also draw instructive conclusions. They represent the transition to the higher vertebrates, in which the middle and older stages of ancestral development have been either destroyed or curtailed, but in which we find the more recent stages of the phylogenetic process well-preserved in memory. We are then in a position to form a fairly complete view of the past development of man's ancestry, when the evidence comes by putting together and comparing the phylogenetic development of the various groups of vertebrates. And so here we get below the low vertebrates, and compare their embryology with that of the higher vertebrates. We can follow the phylogenetic line of our natural environment northward, down to the very upper groups of animals.

In viewing the above path of phylogenetic development, clinging to the biological thread of the historical law and guided till the light of comparative embryology, we will find, in accordance with the methods we have adopted, dissolve and converge these fragments from the manifold history and development of very different animals from which the history of man can be composed. I could call attention particularly to the fact that

employ this method with the same confidence and right as the geologist. No geologist has ever had clearer proof that the vast rocks that compose our Carboniferous or Jurassic or Cretaceous strata were really deposited in water. Yet no one doubts the fact. Further, no geologist has ever learned by direct observation that these various sedimentary formations are deposited in a certain order.

These various sedimentary formations are deposited in a certain order, yet all are sorted as to their order. This

cannot be rationally understood unless they are sorted. These hypotheses are good enough for geologists.

the same value, for the same reason. In formulating them we are acting on the same inductive and deductive methods, and with almost equal confidence, as the geologist. We hold them to be correct, and claim the status of "biological theories" for them, because we cannot understand the nature and origin of these, and the other organisms, without them,

#### knowledge of a biological hypothesis.

In eighteenth century, and more universally limited, so our phylogenetic hypotheses, which are still regarded as farcical in certain quarters, will never or have been generally received. It is true that, as all you say, our task is not to imitate that of the geologists. It is just a much more difficult and complex, as man's organization is more elaborate than the structure of the rocks.

When we approach this task, we find a auxiliary of the utmost importance in comparative anatomy and embryology of the lower animals. One of these animals is the lancet (*Amyda*), the other the sea-squirt (*Aplidium*). Both of these animals are very instructive. Both are at the border between the two chief divisions of the animal kingdom—

*Vertebrates*. The second, the lancet, is the only mentioned

(crustacea, lampreys, fishes, diplopods, amphibia, reptiles, birds, and mammals). Following the example of Leuckart, it is usual to put all the other animals together under the head of invertebrates. But, as I have often mentioned already, the group

is composed of a number of very different stems. Of these we have no interest just now—*annelids*, *molluscs*, and *articulates*, as they are independent branches of the animal-tree, and have nothing to do with the vertebrates. On the other hand, we are greatly concerned with a very interesting group that has only recently been carefully studied, and that has

#### the vertebrates.

the wings of the Tunicates. One of this group, the sea-squirt, very closely approaches the lowest vertebrates, the Amphioxus, in its essential internal structure and embryonic development. Until one had any idea of the close connec-

tions, it was a very fortunate accident that the embryology of these related forms was discovered just at the time when the question of the descent of the vertebrates from the invertebrates came to the front. In order to understand it properly, we must first consider these remarkable animals at their fully-developed forms, and compare their anatomy.

It lives on the flat, sandy parts of the Mediterranean coast, partly buried in the sand, and is apparently found in a number of seas. It has been found in the North Sea (on the British and Scandinavian coasts and to Heligoland) and at various places on the Mediterranean (for instance, in Sicily, Naples, and Messina). It is also found on the coast of Brazil and in the most distant parts of the Pacific Ocean (the coast of Peru, Bolivia, China, Australia, etc.). Recently eight to ten species of the amphioxus have been determined, distributed in two or three genera.

Johannes Müller classed the lancet with the fishes, although he pointed out that the differences between this simple vertebrate and the lowest fishes are much greater than between the fishes and the amphioxus. But this was far from expressing the real significance of the animal. Let us definitely lay down the following principle: The *Amphioxus* differs more from the fishes than the fishes do from

\* See the article *Lancet* by Arthur Willey, *Encyclopaedia Britannica*.

man and the other vertebrates. As a matter of fact, it is no different from all the other vertebrates in its whole organization.

This type is the Acanthia (Ascidians and its extinct relatives), and is the Craniota (fishes and the other vertebrates). The



Fig. 200.

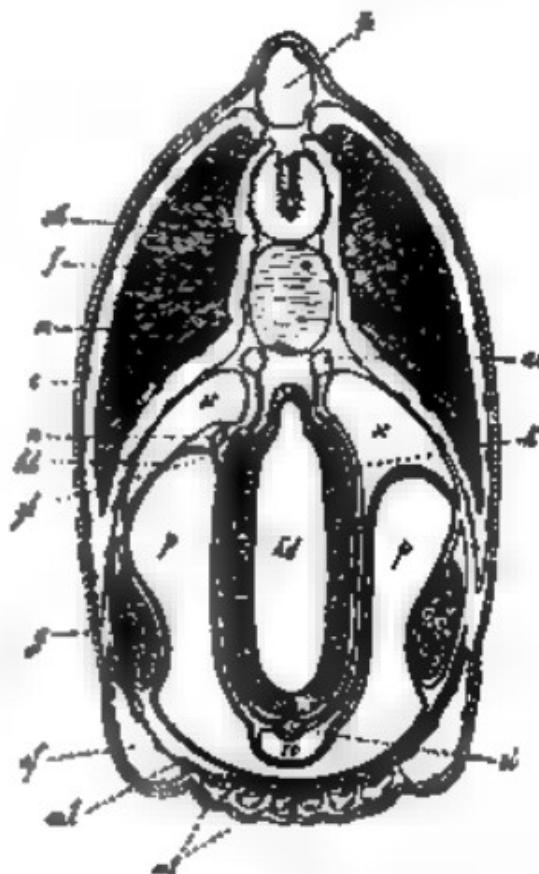


Fig. 201.—Transverse section of the head of the amphioxus. (From Ziegler.)

The long axis.

*A*, mouth of buccal; *B*, nasal; *C*, pharyngeal; *D*, foregut; *E*, neural groove; *F*, neural canal; *G*, branchial vesicle; *H*, branchial fold; *I*, ventral afferent artery; *J*, myomere; *K*, dibranchiate; *L*, right dorsal; *M*, left

Fig. 202.—Transverse section of the head of the amphioxus. (From Ziegler.) In the pharynx, where there are several folds on which we can distinguish the valvulae, above against the dorsal fin (F.G.). To the right and left above, the opercular plates (P); below, in the hypophysis the gonads (G); on each side, the oesophagus (O); in front of the lobules, the branchial vesicles; *M*, junction between the valvulae, *N*, the right dorsal; *O*, the left dorsal; *P*, the subchordal body-wall.

tion that the laws of logical classification impel us to distinguish two divisions or

lancelet). Of these the only living amphioxines are the Amphioxus and Pteropeltis, though there must have been a number of different species at an early period of the world's history.

Opposed to the lancelets is the second division of the vertebrates, which includes all the other members of the class, from the fishes up to man. All these vertebrates have a head and brain from the trunk, with a skull of cartilage, and bone; all have a segmented body, myomeres, kidneys, etc. Hence they are called the Craniata. These last classes are, however, related a great deal more closely. As we already know from our physiology, these three, like every other mammal, pass through the stages of the development of the embryo, which are (1) the cleavage, (2) the blastula stage, (3) the neurula stage, (4) the neural tube, (5) the neural fold, (6) the neural groove, and (7) the formation of the primitive nervous system, the myomeres, brain, etc., of the embryo, until last for a long time the simple form of a hatched chick or a small embryo larva or caterpillar. When we compare this embryonic condition, the undeveloped larvae, with the developed mammals, we may say that the amphioxus has, in a certain sense, a permanent paediatric condition, or a permanent embryonic state of the body. It does, however, show a low grade of development which the larva long since passed.

The fully developed larvae (Fig. 262) is about two inches long, is exteriorized at a right angle, and has the shape of a narrow brown pointed tail. The body is pointed at both ends, but much more pointed at the other. There is no eye or nose. The outer skin is very thin and delicate, naked throughout, a combination of two different layers, a simple external covering of cells, the epidermis, and a thin underlying ectoderm. Along the middle line of the body runs a narrow foldings which projects toward both dorsal and the ventral surface below in a short sacculus. The foldings are supported by a number of minute elastic fibres.

In the middle of the body we find a thickening of the skin, which gives the whole length of the body from front to back, and is pointed at both angles (Fig. 263). This simple extension and thickening is represented by a band in the caudal end of the adult amphioxus. At the anterior this is the only trace of a cerebral column. The dorsal development is further, but rather

less complete throughout the body, as indicated by a few scattered, irregular patches of skin, the dorsal, the ventral, and the lateral. The dorsal and ventral skin are continuous in the middle stage during their life, as a cycloform skin, remaining while above each gill-slit at either end, and meeting in a narrow point in the mid-line. Moreover, the dorsal and ventral skin are continuous, and constitute a small, almost imperceptible hollow supporting of the mouth. This stage is regarded as the beginning of a rudimentary brain. At the foremost end of it there is a small black pigment-spot, a rudimentary eye, and a minute nostril, located in a distinctened eminence. In the vicinity of this spot there is also a small oval, well-defined depression, the single olfactory organ. There is no sign of breathing. The anterior development of the body corresponds to probably, to the mouth, nostril, and eye of the larva, but a mass of degeneration.

Opposite the oral end of the skin there is a very simple alimentary canal, a tube that opens on the ventral side of the mouth by a mouth in front and two behind. The oral mouth is surrounded by a ring of tentacles, on which there are usually two hairy conical processes, the ligaments of mouth. Farther on, the alimentary canal divides into two tubes of about equal length by a constriction in the middle. The fore portion, or hind-gut, serves for assimilation, the hind portion, or rectum, for excretion. The latter of the two alimentary regions is also the seat of the two parts of the body, the head and the trunk. The head is situated just before a broad gill-slit, the greatest width of which is indicated by numbers of 1700 (Fig. 263). The free edge of the gill-slits between the slits are strengthened with four pointed rods, and these are connected by pairs of connectives. The water then enters the mouth of the Amphioxus passes through these slits into the large corresponding branchial cavity, or atrium, and then goes out behind through a hole in the posterior part of the body, the opercular pore (Fig. 263, 264). Below on the ventral side of the gill-slits there is in the middle

line a ciliated groove with a glandular wall (the hypobranchial groove), which is also found in the Acanthia and the larvae of the Cyclostoma. It is interesting because

thyroid gland in the larynx of the higher vertebrates (underneath the "Adam's apple") has been developed from it.

Behind the respiratory part of the gut

or liver (hepatic) gut. The small particles that the *Amphioxus* takes in with the water—infusoria, diatoms, particles of decomposed plants and animals, etc.—goes from the gill-clefts into the digestive part of the canal, and are used up as food. There is a somewhat enlarged portion, that corresponds to the stomach (Fig. 210 A), a long, pouch-like blind sac proceeds straight forward (//). It has

growing in their whole length, and thus driving the circulatory blood through the entire body. On the under-side of the gill-cleft, in the middle line, there is the trunk of a large vessel that corresponds to the heart of the annelides and the trunk of the artery that proceeds from it; the

number of small muscular arculæ, each side from this branchial artery, and form little heart-shaped twilights or *lacunæ* (m) at their points of departure; they advance along the branchial arches, between the gill-clefts and the fore-gut, and divide, on a branchial vein, above the gill-clefts in a large trunk blood-vessel that runs under the dorsal dibrain. This is the principal artery of primitive

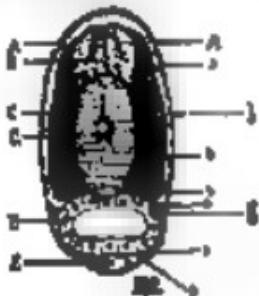


FIG. 210.

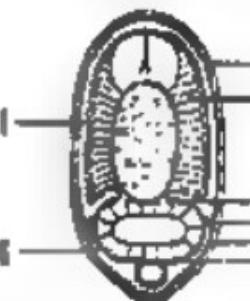


FIG. 210.—TRANSVERSE SECTION OF AN AMPHOXUS LARVA, WITH THE GILL-CLEFTS THROUGH THE MIDDLE OF THE BODY.  
FIG. 210.—TRANSVERSE SECTION OF THE HEAD OF AN AMPHOXUS LARVA.—1, EPIDERMIS; 2, MOUTH TUBE; 3, THROAT; 4, NERVE-SHEATH; 5, HEAD VESICLE; 6, COELOM; 7, MUSCLE LAYER; 8, NERVOUS BODY; 9, OPTIC VESICLE (RETINAL BODY CAVITY).

on the left side of the gill-cleft, and ends blindly about the middle of it. This is the liver of the *Amphioxus*, the simplest kind of liver that we meet in any vertebrate. In man also the liver develops, as we shall see, in the shape of a pouch-like blind sac, that forms out of the alimentary canal behind the stomach.

The formation of the circulatory system in this animal is not less interesting. All the other vertebrates have a compacted, thick, pouch-shaped heart, which develops from the wall of the gut at the throat, and from which the blood-vessels proceed; in the *Amphioxus* there is no special crystallized heart, driving the blood by its pulsations. This movement is effected, as in the annelids, by the thin blood-vessels themselves, which discharge the function of the heart, contracting and

expanding in their whole length, and thus driving the circulatory blood through the entire body. On the under-side of the gill-cleft, in the middle line, there is the trunk of a large vessel that corresponds to the heart of the annelides and the trunk of the artery that proceeds from it; the number of small muscular arculæ, each side from this branchial artery, and form little heart-shaped twilights or *lacunæ* (m) at their points of departure; they advance along the branchial arches, between the gill-clefts and the fore-gut, and divide, on a branchial vein, above the gill-clefts in a large trunk blood-vessel that runs under the dorsal dibrain. This is the principal artery of primitive

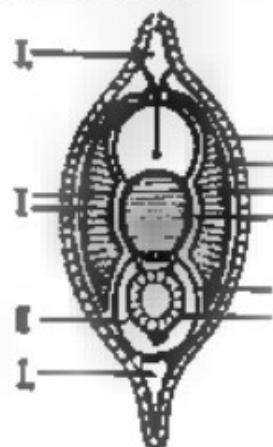
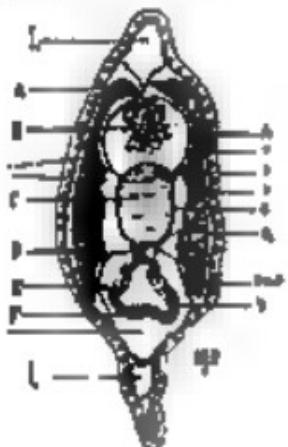
anterior (Fig. 214 B). The branches which it gives off to all parts of the body unite again in a larger venous vessel at the under-side of the gut, called the subventral vein (Figs. 210 B, 212 A). This single main vessel of the *Amphioxus* goes like a closed circular water-conduit along the alimentary canal through the whole body, and pulsates in its whole length above and below. When the upper tube contracts the lower one is filled with blood, and vice versa. In the upper tube the blood flows from front to rear, then back from rear to front in the lower vessel. The whole of the long tube that runs along the ventral side of the alimentary canal and contains venous blood may be called the "principal vein," and may be compared to the ventral vessel in the worm. On the other hand, the long

straight vessel that runs along the dorsal line of the gut above, between it and the chorda, and contains arterial blood, is clearly identical with the aorta or principal artery of the other vertebrates; and on the other side it may be compared to the dorsal vessel in the worms.

The coeloma or body-cavity has some very important and distinctive features in the Amphioxus. The embryology of it is more instructive in connection with the stem-history of the body-cavity in man and the other vertebrates. As we have already seen (Chapter X), in these the two coelom-patches are divided at an early stage by transverse constrictions

(Fig. 216 A). As a matter of fact, this coelom (formerly called the peribranchial cavity) is a secondary structure formed by the development of a couple of lateral folds or gill-cavities ( $M_1, U$ ). The body-cavity ( $L_4$ ) is very narrow and entirely closed, lined with epithelium. The peribranchial cavity ( $A_1$ ) is full of water, and its walls are lined with the skin-sense layer; it opens outwards in the nose through the respiratory pore (Fig. 216 C).

On the inner surface of these muscifolds ( $M_1$ ), in the ventral half of the whole mantle cavity (atrium), we find the sex-organs of the Amphioxus. At each



*Transverse sections of a young Amphioxus, passed through the metapleural, through the intestine, the gonopore and the rectum. The exo-diagram of pharynx,  $I$ , gut,  $II$ , rectum.  $A$ , auxiliary tube,  $B$ , ductus,  $C$ , dorsal oesophagus,  $D$ , ventral oesophagus,  $E$ , anterior rectal canal,  $F$ , posterior rectal canal,  $G$ , proctodaeal tube,  $H$ , mesophore,  $I$ , pharynx,  $J$ , dorsal fin,  $K$ , ventral fin.*

into a double row of primitive segments (Fig. 215), and each of these solidules, by a frontal or lateral constriction, into an upper (dorsal) and lower (ventral) pouch.

These important structures are seen clearly in the trunk of the amphioxus (the latter third, Figs. 212-215), but  $\text{II}$  is otherwise in the head, the foremost third (Fig. 216). Here we find a number of complicated structures that cannot be understood until we have studied them on the embryological side in the next chapter (cf. Fig. 81). The buccal vent is here fused in a common cavity filled with water, which was wrongly thought formerly to be the body-cavity (Fig.

vale of the buccal gut there are between twenty and thirty roundish four-sided vales, which can clearly be seen from without with the naked eye, as they shine through the thin transparent body-wall. These vales are the sexual glands; they are the same size and shape in both sexes, only differing in contents. In the female they contain a quantity of simple ova (Fig. 219 A), in the male a number of much swollen cells that change into mobile ciliated cells (sperm-cells). Both vales lie on the inner wall of the atrium, and have no special outlets. When the ovaries are ripe, they fall into the atrium through the gill-clefts into the f

gut, and are ejected through the mouth.

Above the sexual glands, at the dorsal angle of the atrium, we find the kidneys. These important excretory organs could not be found in the Amphioxus for a long

time, and are ejected through the mouth. Their internal aperture (Fig. 217 B) opens into the body-cavity; their outer aperture into the atrium (C). The proventral canals lie in the middle of the line of the head, outwards

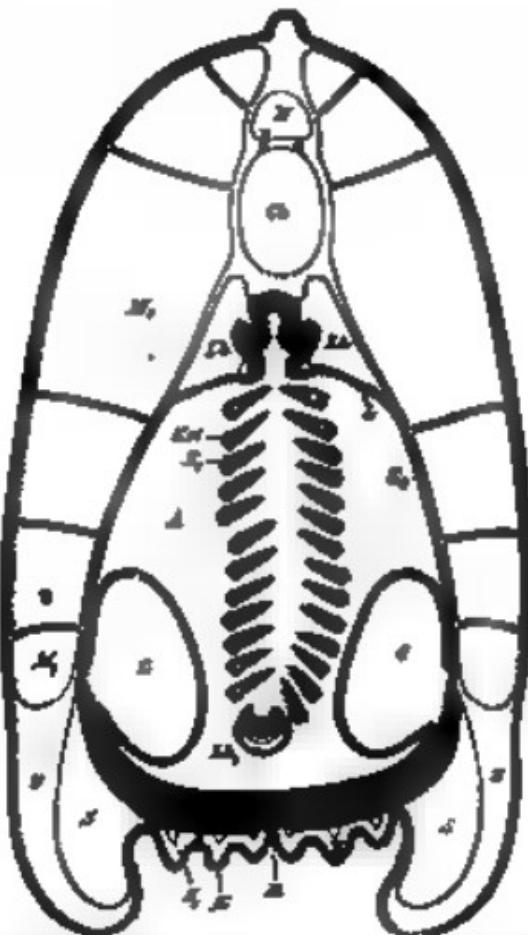


FIG. 217.—Transverse section of the lancelet, in the dorso-lateral view (from Bovier). The white covering is the epidermis of the skin. Under this is the thin meso-, the endostomes layers of which are represented by the black lines between the rows of dots, and in the circulations. It consists of two rows of dots, 2 mm. and 3 mm. in every mill. of surface. (See also Fig. 216.)

time, on account of their remote position and their smallness; they were discovered in 1890 by Theodor Boveri (Fig. 217 x). They are short segmental canals, corresponding to the primitive kidneys of the

man the segmental nature of the gill-slits, and bears important relations to the haemal vessels (*H*). For this reason, and in their whole arrangement, to primitive kidneys of the Amphioxus

show clearly that they are equivalent to the proرانal canals of the Craniates (Fig. 218 B). The proرانal duct of the lancelet (Fig. 218 C) corresponds to the branchial cavity or atrium of the former (Fig. 217 C).

If we sum up the results of our anatomic study of the Amphioxus, we

both animals in the same division of the animal kingdom. Nevertheless, this classification is indisputably just. Man is only a more advanced stage of the vertebral type that we find unrelatably in the Amphioxus in its characteristic features. We need only recall the : of the still primitive Vertebrates

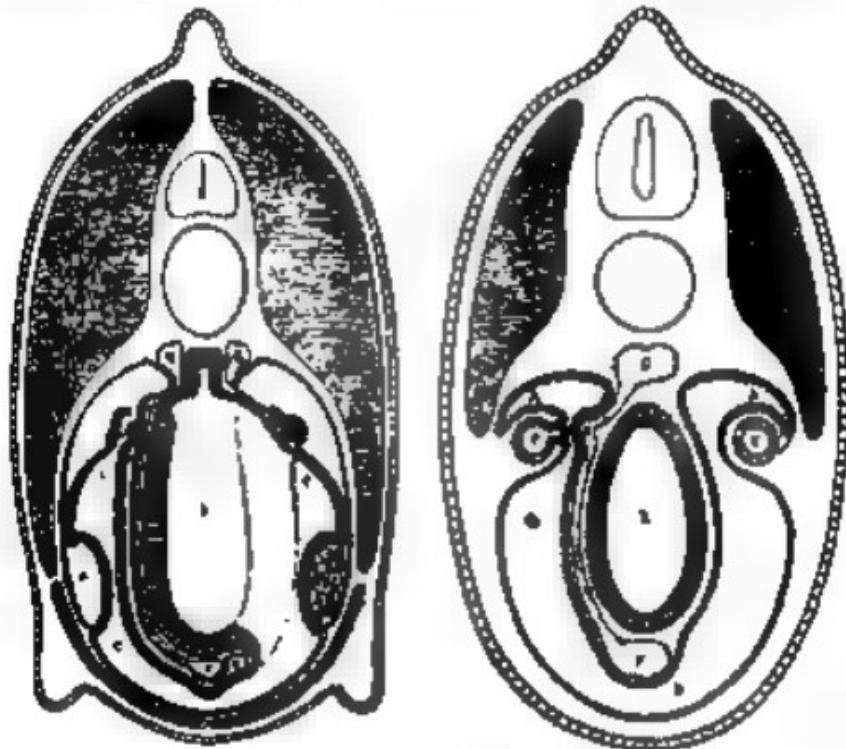


FIG. 217.—*Dorsiventral sections through the middle of the Amphioxus.* (From Herdman.) On the left a general line has been struck, and on the right a placid; consequently on the left we see the whole of a cerebral canal (A), on the right only the portion of a broader, a general chamber (B) ventral aspect of the forebrain, a prosomere. At the rhombencephalic division, A, hindbrain; E, ventral ganglion; F, ventral nerve cord; G, neural canal.

compare them with the familiar organization of man, we shall find an immense distance between the two. As a fact, the highest summit of the vertebrate organization which man represents is at every respect so far above the lowest stage, at which the lancelet remains, that one would at first scarcely believe it possible to class

the amphioxus with the higher vertebrates. The dotted lines on the right indicate the later openings of the prosomere below, namely F (4) and the proرانal duct (C), D, hindbrain; E, ventral cavity; F, subventral vein; G, canal, G, neural canal.

given in a former chapter, and compare it with the lower stages of human embryonic development, to convince ourselves of our close relationship to the lancelets. (See Chapter XI.)

It is true that the Amphioxus is far below all other living vertebrates. It is true that it has no separate head, no developed brain or skull, the characteristic feature of the other vertebrates,

It is (probably as a result of degeneration) without the respiratory organs and the centralised heart that all the others have; and it has no fully-formed kidneys. Every single organ is as it is simple and less advanced than in any of the others. Yet the characteristic connection and arrangement of all the organs is just the same as in the other vertebrates. All these, moreover, pass, during their embryonic development, through a stage in which their whole organisation is no higher than that of the Amphioxus, but is substantially identical with it.



Diagram of a Lancelet (Cyclostoma) showing the arrangement of its internal organs. It is a transverse section of the body, showing the pharynx, gut, and various internal organs. The diagram is labeled with letters A through Z, corresponding to the labels in the text below.

In order to see this quite clearly, it is particularly useful to compare the Amphioxus with the youngest forms of these vertebrates that are classified next to it. This is the class of the Cyclostomes. There are to-day only a few species of

be distributed in two groups. One group comprises the lampreys or Myxines. The other group are the Petromyzontes, which are a

familiar sight in their marine form. These Cyclostomes are usually classified with the fishes, but they are far below the true fishes, and form a very interesting connecting-group between them and the lancelet. One can see how closely they approach the latter by comparing a young lamprey with the Amphioxus. The chorda is of the same simple character in both, also the mandibular tube, that opens above the pharynx, and the oral disc is, however, in the lamprey the spiral cord divides in front into a simple pear-shaped cerebral vesicle, and at each side of it there are a very simple eye and a rudimentary auditory vesicle. The nose is a single pit, as in the Amphioxus. The two sections of the gut are also just the same and very rudimentary in the lamprey. On the other hand, we see a great advance in the structure of the heart, which is found underneath the gut, in the shape of a centralised muscular tube, and is divided into an auricle and a ventricle. Later on the bronchi, which will further, and give a small, the cerebral vesicle, a series of independent gill-pouches. This makes all the more for the striking resemblance of the immature larva in the developed metamorphosed mature Amphioxus.

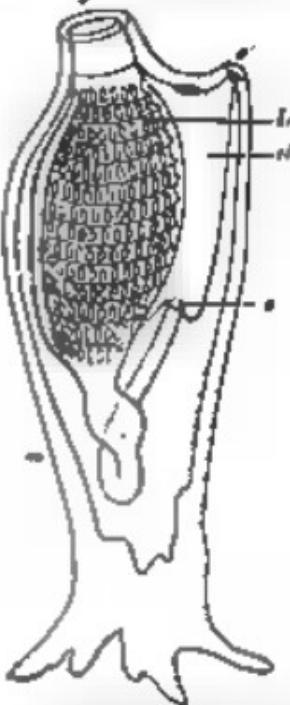
While the Amphioxus is thus connected through the Cyclostomes with the fishes, and so with the series of the higher vertebrates, it is, on the other hand, very closely related to a lowly invertebrate marine animal, from which it seems to be easily separable at first glance. This remarkable animal is the Ascidia or Ascidian, which was formerly thought to be closely related to the mollusc, and so stand in the mollusc. But since the remarkable embryo stage of these animals was discovered in 1900, there can be no question that they have nothing to do with the mollusc. To the great astonishment of zoologists, they were found, in their whole individual development, to be closely related to the vertebrates. When fully developed the Ascidians are singular forms that could not, at first sight, be taken for vertebrates at all. The adult body, frequently studded with knobs or tufts and bumps, in which we can discover no special external regularity,

or the floor of the sea. Many species look like potatoes, others like onion-casts, others like pebbles. Many of the Ascidians form transparent crusts or

deposits on stones and marine plants. Some of the larger species are eaten like oysters. Fishermen, who know them very well, think they are not animals, but plants. They are sold in the fish markets of many of the Indian coast-ports with other lower marine animals under the name of "sea-fruit" (*fruits de mer*). There is nothing about them to show that they are animals. When they are taken out of the water with the net the sweet one can perceive a slight contraction of the body that causes water to spout out in two places. The bulk of the Acantho-aria are very small, at the most a few inches long. A few species are a foot or more in length. There are many species of them, and they are found in every sea. As in the case of the Ascidia, we have no fossilized remains of the class, because they have no hard and fossilizable parts. However, they must be of great antiquity, and must go back to the pre-vertebral epoch.

The name of "Tunicates" is given to the whole class to which the Acantho-aria belong, because the body is enclosed in a thick

secreted by the large grated branchial sac (*dr.*). This is so like the gill-craze of the Amphioxus in its whole arrangement that the resemblance was pointed out by the English naturalist Goodir, years ago, before anything was known of the relationship of the two animals. As a fact, even in the Acantho-aria the mouth (*o.*) opens first into this wide branchial



The diagrammatic representation of an Acantho-aria (left view). The dorsal side is turned to the right, and the ventral

side to the left. The mouth (*o.*) above, is situated at the tail end. The branchial sac is formed by a number of slits, over the ventral side. The rectal opening (*Ir.*) is at the stomach end. The excretory pores (*v.*) are placed with the respiratory pores (*dr.*) on the branchial or cloacal flap, at the Cephalic end.

that have a real cellulose or waxy coat. Sometimes the cellulose substance is brightly colored, all other times colorless. Not infrequently it is set with steriles or hairs,

#### THE ANEMONE AND THE CORAL-REEF

The hind end, which corresponds to the tail of the Amphioxus, is usually flattened, often by means of regular roots. The dorsal and ventral sides differ a good deal internally, but frequently cannot be distinguished externally. If we open the thick tunica or mantle in order to examine the internal organization, we find first a spacious cavity filled with water—the mantle-cavity or respiratory cavity (Fig. 220 *c.*). It is also called the branchial cavity and the cloaca, because it receives the excrements and sexual products as well as the respiratory water. The greater part of the respiratory cavity is

occupied by the large grated branchial sac (*dr.*). This is so like the gill-craze of the Amphioxus in its whole arrangement that the resemblance was pointed out by the English naturalist Goodir, years ago, before anything was known of the relationship of the two animals. As a fact, even in the Acantho-aria the mouth (*o.*) opens first into this wide branchial

consists of tiny organisms, infusoria, diatoms, parts of decomposed marine plants and animals, etc. These pass with the water into the gill-cavity and the digestive part of the gut at the end of it, at first into an enlargement of it that represents the stomach. The adjoining small intestine usually forms a loop, bends forward, and opens by an *anus* (Fig. 220 *a*), not directly anterior, but fine into the mantle cavity; from this the secretions are ejected by a common outlet (*a'*) together with the food-up



*a*—Anatomical diagram of an ascidian (Fig. 220). *b*—Longitudinal section of an ascidian (Fig. 221).

#### THE BRANCHIAL CLEFTS OF THE ASCIDIAN (From Haeckel's *Zoologie*)

water and the sexual products. The outlet is sometimes called the *branchial pore*, and sometimes the cloacal or *ejective-aperture*. In many of the *Arcellina* a glandular mass opens into the gut, and this represents the liver. In some there is another gland besides the liver, and this is taken to represent the kidneys. The body-cavity proper, or coelom, which is filled with blood and encloses the hepatic gut, is very narrow in the *Arcellina*, as in the *Amphioxus*, and is here

also mostly confounded with the wide atrium, or peribranchial cavity, full of water.

There is  
Ancestral of  
several classes. It is the more interesting that the young animal that emerges from the mass has a *chorda*, and that there is a rudimentary medullary tube above it. This latter is wholly atrophied in the developed *Arcellina*, and looks like a small nerve-ganglion in front above the gill-cavity. It corresponds to the upper "gullet-ganglion" or "peribranchial brain" in other vertebrates. Special sense-organs are either wanting altogether or are only found in a very rudimentary form, as simple optic spots and touch-corpuscles or unapses that surround the mouth. The muscular system is very slightly and haphazardly developed. Immediately under the *tholo* *stomach*, and closely connected with it, we find a thin muscle

*c*, as in the worms. On the other hand, the *Arcellina* has a *posteriorized heart*.

In this respect it seems to be more advanced than the *Amphioxus*. On the ventral side of the gut, some distance behind the gill-cavity, there is a spindle-shaped heart. It retains permanently the simple tubular form that we find temporarily in the first structure of the heart in the vertebrates. This simple heart of the *Arcellina* has, however, a remarkable peculiarity. It contracts in alternate directions. In all other animals the beat of the heart is always in the same direction (generally from tail to front); it changes in the *Arcellina* to the reverse direction. The heart contracts first from the rear to the front, stands still for a moment, and then begins to beat the

alternately an anterior and veins. This square is found in the *Tunicata* alone.

Of the other chief organs we have still to mention the sexual glands, which lie right behind in the body-cavity. All the *Arcellina* are hermaphrodites. Each individual has a male and a female gland, and so is able to fertilize itself. The eggs (*e*; *e'*) fall directly from the ovaries (*o*) into the mantle-cavity. The *male ductus is considerably longer* than the *female* (*f*), by a special duct (*f'*). Fertilization is accomplished here, and in many of the *Arcellina* developed embryos are found. These are (ben-

Elect with the breathing-water through the cloaca (q), and so "born alive."

If we now glance at the entire structure of the simple Ascidia (especially *Phallusia*, *Cynthia*, etc.) and compare it with that of the Amphioxus, we shall find that the two have few points of contact. It is true that the fully-developed Ascidia resembles the Amphioxus in several important features of its internal structure, and especially in the peculiar character of the gill-slits and gut. But

in most other features of organization it is as far removed from it, and is so unlike it in external appearance, that the really close relationship of the two was not discovered until their embryology was studied. We will now compare the embryonic development of the two animals, and find to our great astonishment that the same achaean form develops from the ovum of the Amphioxus as from that of the Ascidia—a typical chordate.

## CHAPTER XVII.

### EMBRYOLOGY OF THE LANCELET AND THE SEA-SQUIRT

so prominent that there was the greatest difficulty in the earlier stages of classification in determining the affinity of these two groups of organisms. When scientists began to speak of the affinity of the various animal groups in more than a figurative—*i.e.* a genealogical—sense, this question came at once to the front, and seemed to constitute one of the chief obstacles to the carrying-out of the evolutionary theory. Even earlier, when they had studied the relations of the chief groups, without any idea of real genealogical connection, they believed they had found here and there among the invertebrates points of contact with the vertebrates. . . . of the vertebrates, especially, we used to approach the vertebrates at structure, such as the marine arrow-worm (*Sagitta*). But on closer study the analogies proved untenable. When Dohrn gave an impulse to the construction of a real history of the animal kingdom by his reform of the theory of evolution, the solution of this problem was found to be particularly difficult. When I made the first attempt in my *General Morphology* (1866) to work out the theory and apply it to classification, I found no problem of phylogeny that gave me so much trouble

but just at this time the true link was discovered, and at a point where it was least expected. Towards the end of 1866 two works of the Russian Biologist, Kowalevsky, who had lived for some time at Naples, and studied the embryology of the lower animals, were issued in the publications of the St. Petersburg Academy. A fortunate accident had directed the attention of this able observer almost simultaneously to the embryology of the lowest vertebrate, the Amphioxus, and that of an invertebrate, the close affinity of which to the Amphioxus had been least suspected, the Ascidia. To the extreme astonishment of all zoologists who were interested in this important question, there turned out to be the utmost resemblance in structure from the commencement of development between these two very different animals—the lowest vertebrate and the simplest, most invertebrate. With this indubitable identity of ontogenesis, which can be demonstrated to an astounding extent, we had, in virtue of the biogenetic law, discovered the long-sought genealogical link, and definitely identified the invertebrate group that represents the nearest blood-relatives of the vertebrates.

The discovery was confirmed by other workers, and there can no longer be any doubt that all the classes of coelomates that of the Tunicates is most closely related to the vertebrates, and of the Tunicates the ascidians are the Ascidiidae. We cannot say that the vertebrates are descended from the Ascidiidae—and still less the reverse—but we can say that of all the invertebrates it is the Tunicates and within this group, the Ascidiidae, that are the nearest blood-relatives of the earliest descendants of the vertebrates. We can agree on the common ancestral group of both stems as against Lemety of the "prostomes" or Ctenophores, the Pseudocoelomata ("prostomes" Chordomorphi").

In order to appreciate fully this research work first, and especially to notice the chief lines we take for the generalization of the vertebrates, it is necessary to study throughout the embryology of both these groups, and compare the individual development of the Amphioxus with that of the Ascidia. We begin with the embryology of the Amphioxus.

From the considerable observations of Kowalevsky at Naples and Haeckel at Monaco, it follows, briefly, that the segmentation and gastrulation of the Amphioxus is of the cleavage character. This also holds in the same way as is the fact that in many of the larval forms of different invertebrate groups, which we have already described as originally differentiated, the development of the Notochord is of the water-type. Briefly-stated: specimens of the Amphioxus, which are found in great quantities at Monaco from April to May onward, begin as a rule to eject their sexual products in the evening; if you catch them about the middle of a storm night and put them in a glass covered with water, they immediately open through the mouth their accumulated sexual products, in consequence of the disturbance. This action gives out masses of sperm, and the female discharge over in such quantity that many of them stick to the filaments about their mouths. Both kinds of discharge float into the sea-shore early after the opening of the gonads, pass through the gill-slits into the briny tidal pool, and are discharged from this through the mouth.

The eggs are singly round cells. They are only one-half the size of the ascidian eggs, and two and one-half times the size of the

ova, and have no distinctive features. The clear protoplasm of the ovules even is made to tinted by the number of dark granules of food-yolk or deutoplasm contained in it that it is difficult to follow the process of differentiation and the transition of the two nuclei during it (Fig. 51). The entire contents of the ova, except the yolk-mass or the cellular substance of the egg, make their basal part—the chorion part of the cell right outside the nucleus. Only one yolk-granule occupies the rest of the cell at one part of the protoplasm. In fact, a nucleus disappears with the female nucleus, which occupies when the maturation of the ova comes from the germline vesicle. This is formed by the "oocyte-nucleus," or the nucleus of the "oocyte-cell" (textile, Fig. 5). The two vesicles and yolk-mass, dividing into two, four, eight, sixteen, thirty-two cells, and so on. In this way we get the spherical, radiately-shaped body, which we call the embryo.

The gastrulation of the Amphioxus is not exactly regular, as was supposed after the first observations of Kowalevsky (1866). It is not completely equal, but a little unequal. As Haeckel afterwards found (1874), the segmentation-cells only remain joined up to the mid-dorsal, the spherical body of which consists of thirty-two cells. Then, as always happens in segment gastrulation, the more ventral vegetal cells are not wrapped in the chorion. At the lower or vegetal pole of the ovule a row of eight large notochordal cells remains for a long time unchanged while the other cells divide, owing to the formation of a series of longitudinal furrows, one an inter-embryonic member of rows of eleven cells each. Above and the segmentation-cells get older or less regularly developed, while the segmentations-cells undergo in the center of the ovule, in the end moreover all lie on the surface of the latter, so that the latter retains the familiar bilobate shape and form.

The wall of a fresh embryo is a single sheet of cells (Figs. 52 A-C). This layer in the Monostoma, the single addition over the rest of eight or ten layers of the body present.

These important early developments prepare two pieces of anatomy in the Amphioxus that four or five hours after gastrulation, or about midnight, the spherical Morula is completed. A pit-like depression is then formed at the vegetal pole of it, and in consequence of this the hollow yolk-sac泡 is made (Fig. 26, A). The pit becomes deeper and deeper (Fig. 26 A, B); it has the invagination (or budding) incomplete, and the lower folded part of the blastoderm-wall lies on the inside of the outer wall. We thus get a hollow haemophore, the thin wall of which is made up of the layers of cells (Fig. 26 C). From hereon follows the very same histories almost spherical morula, and then all the internal cavity enlarging considerably and its mouth opening narrow (Fig. 26 D). The form which the haemophore reaches has been called a "two-layered" or "gastrula" of the original Amphioxus; it has however already developed an "endostyle" or "stomaphore" (Fig. 26 E).

In all the other animals that have an endostome, the whole body is nothing but a simple groove and its mouth, internal cavity in the primitive gut (prostomia or entoderm), Fig. 26 G, 26 H, and its apertures the primitive mouth (prostome or stomaphore, 2). The wall is at once gut-wall and body-wall. It is composed of two simple substances, the inner or primary protostomial layer. The outer layer is the invaginated part of the blastoderm, which immediately covers the gut-lumen in the entoderm, the outer or vegetal gastrula-layer, from which derives the wall of the alimentary canal and all its appendages, the excretive canals, etc. (Figs. 26, 28, 29, 3). The outer surface of cells of the outer invaginated part of the blastoderm, in the primitive gut, is called the ectoderm, or outer or animal gastrula; a fact provides the outer skin (epidermis) and the nervous system (3). The cells of the ectoderm are much larger, thicker, and more fully than those of the entoderm, which are clearer and less rich in fatty particles. Hours before and during gastrulation there is an interesting differentiation of the inner from the outer layer. The animal cells of the outer layer carry sharp ciliated hairs; the vegetal cells of the inner layer do not reach later. A third-like primary groove set of such cells, and often containing ciliated hairs, comes down as grooves of the Amphi-

xous surface above in the one, when it has ploughed the thin entoderm, like the epidermis of many other animals (Fig. 28). As in every other lower animal, the cells have only one ciliated hair each and are called flagellata (which agrees in contrast with the ciliated cells, which have a number of short hairs or cilia).

In the further course of the rapid development the roundish ball-gastrula becomes elongated, and begins to flatten on one side, parallel to the long axis. The flattened side is the subsequent dorsal side; the opposite or ventral side remains curved. The latter grows more rapidly than the former, with the result that the primitive mouth is fixed to the dorsal side (Fig. 26 H). In the middle of the dorsal surface a shallow longitudinal groove or furrow is formed (Fig. 26 I) and the edge of the body rises up on each side of this groove in the shape of two parallel foldings. This groove is, of course, the dorsal furrow, and the foldings are the dorsal or myodermic protostomia; they form the first sacrum of the nervous system of man, the medullary canal. The myodermic foldings bear the thicker, the epaxial band on their inner surface and deeper. The edges of the parallel foldings move towards each other and at last meet, and the medullary tube is formed (Figs. 26 J, K, L, 28, 29). Hence the formation of a median tube out of the outer lips which pass on the ventral surface of the body covering lumen of the Amphi-xous as far as the mouth (4), as we have found in the study of that and the higher animals after the dorsal evagination.

Concurrently with the evagination of the medullary tube the bone in the vertebral column, the cartilage of the chorda, the cartilaginous, and the epiphyses growing from them (5). These processes take place with characteristic simplicity and clearness, so that they are very instructive to compare with the epiphyses on the one hand and with the higher vertebrates on the other. While the medullary groove is starting in the middle line of the flat dorsal side of the Amphi-xous, and its parallel folds are to form the vertebral column, the single chorda is turned directly upwards from, and on each side of the pre-embryonic region, laid down the epiphyses of the vertebral gas. These longitudinal folds of the vertebral groove bear the pharyngeal mouth, or from the base

and blinder edge. How we see at our early stage a couple of large ectodermic cells, which are distinguished from all the others by their great size, round form, and flagellated protoplasm; they are the two *epiblastes*, or polar cells of the Amphi-

blast (Fig. 51, p.). They indicate the central starting-point of the two dorsal and ventral edges, which grow from this spot and pass gradually into the primitive gut, and provide the cellular material for the mid-dorsal layer.

Immediately after their formation the ectodermic patches of the Amphi-

blast are several parts by longitudinal and transverse folds. Each of the

regions is divided into an upper dorsal and a lower ventral section by a couple of lateral longitudinal folds (Fig. 52). But these are again divided by several parallel transverse folds into a number of segments, the primitive segments or somites (formerly called by the Greeks *metathorax* or "primitive vertebrae"). They have a different future above and below. The upper or dorsal segments, the epiblastes, later on lie later on, and form with these cells the muscular plates of the trunk. The lower or ventral segments, the hypoblastes, corresponding to the lateral plates of the Amphi-embryo, that together in the upper part owing to the disappearance of their lateral cells, and thus form the later body-layer (hypoderma), in the lower part they remain separate, and afterwards form the epibranchial groove.

In the middle between the two basal foldoids of the primitive gut, a single central groove develops.

At early stage in the middle line of its dorsal wall. This is the dorsal chorda (Fig. 52, 1, a). This rapid red, often

slight invagination of the later vertebral column in all the vertebrates, and is the only representative of it in the Amphiblast, disappears from the ectoderm.

In consequence of these important thickening-processes in the primitive gut, the single ectodermic tube divides into two different sections:—1., ventral, or ventral side, the permanent alimentary canal or primitive gut; 2. 11.—above, at the dorsal side, the head and a mouth; and III.—the two rudiments, which immediately subdivide into two structures—IIIa., above, on the dorsal side, the epibranches, the double row of primitive or muscular segments; and IIIb., below, on each side of the gut, the hypoblastes,

the two lateral plates that give rise to the eye-glands, and the epibranches which partly unite to form the body-musculature. At this same time the second or mandibular fold is formed above the epibranches, so the dorsal surface, by the closing of the post-larval mandibular foldings. All these processes, which outline the typical structure of the vertebrate, take place with amazing rapidity: at the embryo of the Amphioxus, i.e. the duration of the first day, or twenty-four hours after fertilization, the young amphioxus, the typical

is to night larva.

The other processes on the second day of development in the construction of the

the alimentary tube to found to go rapidly ahead, after the closing of the primitive mouth, is only connected with the mandibular tube. The permanent mouth is a secondary formation, or the opposite end. Here, at the end of the second day, we find a double depression in the outer skin, which connects backwards into the closed gut. The anus is formed behind in the same way a few hours later (in the vicinity of the additional glandular-cell).

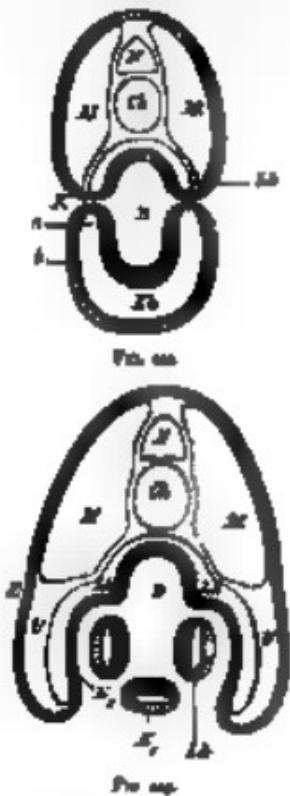
In man and the higher vertebrates, as we have seen, no flat pit on the outer skin, they then penetrate successively, gradually, becoming connected with the blind ends of the closed gut-tube. During the second day the Amphioxus-embryo undergoes few other changes. The number of primitive segments increases, and generally amounts to thirteen, more forty-eight to fifty hours after hatching.

Almost simultaneously with the formation of the mouth the first gill-slits become through in the fore portion of the Amphi-embryo (between forty hours after the commencement of development). It is a series of six slits, which independently, as the last ventral chord, incompletely overlap. The further closing movement of the fore three takes place very slowly, and

The body becomes much longer, and is compressed at the width. The head-and-neck transformed in a sort of triangle. Two rudimentary nerve-organs are developed in it. While we find the first branchials, on upper or dorsal road, corresponding to the cavity between the gut and the dorsal cord, and a layer of ventral

Now, the gills or respiratory organs are formed at the fore-end of the alimentary canal. The whole of the anterior or respiratory section of the gut is converted into a gill-crate, which is pierced medially by numbers of branchial-holes, as in the ascidia. This is done by the fore-end part of the gut-wall joining ventrally with the outer skin, and the formation of clefts

"we have previous  
like Vertebrates" (Figs. 98-102).  
But the body afterwards undergoes various  
modifications, especially in the fore-part.  
These modifications do not concern us, as  
they depend on special adaptations and  
do not affect the hereditary vertebrate  
type. When the free-swimming Amphi-



1 particle of 7 mm  
made from 500000  
nm<sup>2</sup> cm<sup>-2</sup> s<sup>-1</sup>

With the larvae hatching the *Spumellaria* are found, & also *Alcyonium*, *Leptoria*, & *Leptopora*. A part of the body-skins in which the animal organs are subsequently formed, is gut-cavity, covered with the glomerular layer of *Epithelia*. A muscle-cavity, *Muscularis*, & a *Stomach*, & the nervous system, a *Neurula*, are the result of a rapid evolution of the *Spumellaria*, & are personal properties of the *Polypoid* cells.

at the point of connection, piercing the wall and leading into the gut from without. At first there are very few of these branched clefts; but there are soon a number of them—first in one, then in two,

The foremost gill-cleft is the oldest. In the middle of each cleft there is a row of fine gill-clefts, supported on a network of stiff branchial rods; these are connected in pairs by transverse rods.

At an early stage of biological develop-

comes larva, is three months old, it abandons its pelagic habits and changes into the young animal that lives in the sand. In view of its smallness (one-eighth of a inch), it has substantially the same body as the adult. As regards the remaining stages of the *Amphioxus*, we need only mention that the gonads or sexual glands are developed very late, immaturity set in of the lower cell-layer of the

Individually, Aristotle's we can find afterwards no continuation of the body-cavity (Fig. 216 E) in the larval walls of the Amphi-amely. In the pig-tail or amphiolepis (Fig. 224 C), there is one opening in the beginning (Fig. 224 D). The second one is formed later, at the bottom of this continuation (Fig. 224 E). For the rest, the sequence of development into the adult Amphioxus of the larva we have followed is so simple that we need not go further into it here.

We may now turn to the early stage of the Acantho-, an animal that seems to stand as much lower and to be as much more simply organized, especially in the earlier part of its life, attached to the bottom of the sea like a shallow lump. It was a fortunate accident that I was able to find examined just above larger specimens of the Acantho- that there must clearly be a continuation of the ventricle to the atrium, and the body of which below appears like that of the Amphioxus in the first stage of development. This circumstance is to allow us to make inquiries that we have only hitherto been able to make with regard to the development of the Amphioxus.

The stage of the larger Acantho- of that from Crete, we have a single round cell of the size of an egg, a diameter. In the dark greenish pulp we find a clear oval gonadal sac of about one millimetre in diameter and the surface a small, yellowish spot of matter which marks the position that corresponds the vent, the atrium of the Acantho- after differentiation, passes through all the same metamorphoses as the atrium of the Amphioxus. It undergoes local segmentation; it divides into two, four, eight, sixteen, thirty-two cells, and so on by continued local division the ventral, or midventral cluster of cells, is formed. These gather inside it, and then we get once more a globular ventral body-chord; the wall of this is a single layer of cells, the ventricle. A new ventricle is simple but provided a further lining the interior by an epidermis, in the same way as in the amphioxus.

Up to this there is no distinct ground in the embryology of the Acantho- for bringing them into close relationship with the Vertebrates; the mere gonad is formed in the same way in many other groups of different stems. We see but an embryonic process that is peculiar to the Vertebrates, and that process lies

frankly the utility of the Acantho- in the Vertebrates. From the epidermis of the gut, a midventral fold is formed on the ventral side, and, between this and the primitive gut, a chorda. There are the openings that are often not only found in Vertebrates. The formation of these very important organs takes place in the Amphi-amely. In proving the case we are in it that of the Amphioxus. In the Amphi- (as in the other cases the oral epidermis is first detached on one side—the subepidermal dorsal wall). A groove or fissure (the midventral groove) is made in the middle line of the flat surface and a parallel longitudinal swelling runs an entire width from the side later. These midventral swellings join together over the fissure, and form a tube, in this way, ventrally, the ventral or midventral tube is at first open to the outside, and connected with the primitive gut behind by the midventral canal. Further, in the Amphi-amely also the two prominent apertures of the stomatocyst and rectal appear later, at independent and new positions. The rectal mouth does not develop from the primitive mouth of the gut itself, this latter mouth closes up, and the later tube is formed near it by invagination from without, on the hinder end of the body, opposite to the aperture of the midventral tube.

During these important processes that take place—just the ventricle of the Amphi-amely, a relative proportion goes out of the ventral end of the larva, which, with the ventral fold, will give birth the ventral epidermis to which is due that the dorsal side is turned and the tail is turned to the ventral side. On the tail is developed starting from the primitive gut a cylindrical ring of cells, the fate of which makes the body of the Amphi- between the anterior end and the ventral mouth and is no wider than the chordal diameter. This important organ had hitherto been found only in the Vertebrates, not a single trace of it being discernible in the Amphi-amely. At first the chorda only consists of a single row of large, nucleated cells. It is afterwards composed of several rows of cells. In the Amphi- larva, also, the chords do come from the dorsal middle part of the primitive gut, where the two endodermic dorsal pouches lie front to back side. The simple body-cavity is formed by the amniogenesis of the two.

When the Amphi-amely has attained

this stage of development it begins to move about in the ovicavity. This causes the membrane to burst. The larva emerges from it, and swims about free of its own-like tail.

These free-swimming larvae have been known for a long time. They were first observed by Darwin during his voyage round the world in 1832. They resemble tadpoles in outward appearance, and use their tails as oars, as the tadpoles do. However, this lively and highly-developed condition does not last long. At first there is a progressive development, the foremost part of the muscular tube enlarges into a brain, and inside this two single vesicles are developed, a dorsal auditory vesicle and a ventral eye. Then a heart is formed on the ventral side of the animal, or the lower wall of the gut, in the same simple form and at the same spot at which the heart is developed in man and

adult, spool-shaped

birds and, as in the case with the adult Anelids. In this way the sanguiferous fluid accumulated in the hollow muscular tube is driven in alternate directions into the blood-vessels, which develop at both ends of the aortic tube. One principal vessel runs along the dorsal side of the gut, another along its ventral side. The former corresponds to the aorta and the dorsal vessel in the worms. The other corresponds to the subintestinal vein and the ventral vessel of the worms.

With the formation of these organs the progressive development of the Acanthocephala comes to an end, and degeneration sets in. The free-swimming larva sticks to the floor of the sea, abandons its locomotive habits, and attaches itself to stones, marine plants, mussel-shells, corals, and other objects; this is done with the part of the body that was formed in movement. The attachment is effected by a number of out-growths usually three, which can be seen even in the free-swimming larva. The tail is lost, as there is no further use for it. It undergoes a fatty degeneration, and disappears with the choctus dorsalis. The latter body changes into an unshaped tuft, and, by the atrophy of some parts and the modification of others, gradually

assumes the appearance we have already described.

Among the living Tunicates there is a very interesting group of small animals that swim throughout life at the stage of development of the tailed, free Acanthocephala, and swim about briskly in the sea by means of their broad car-tail. These are the remarkable Cephalata (*Aplidium*,



FIG. 242.—An Acanthocephala (Diplopeltis), seen from behind. a, dorsal vesicle; b, branchial gut; c, gut; d, stomach; e, heart; f, ventral vesicle under the gut; g, nervous system; h, afferent nerve; i, dorsal; j, tail.

*caviceps* and *Festucalex*, Fig. 245). They are the only living Vertebrates that have throughout life a choctus dorsalis and a nervous string above it, the latter must be regarded as the prolongation of the cerebral ganglion and the equivalent of the muscular tube. Their branchial gut also opens directly outwards by a pair of

branchial clefts. These instructive Capitata, comparable to permanent Ascidio-larvae, come next to the extinct Proterostomia, those ancient worms which we must regard as the common ancestors of the Tunicates and Vertebrates. The heart of the Apylomimetic is a long, cylindrical tube (Fig. 202, r), and moves as an attachment for the muscles that work the flat ear-tail.

Among the various modifications which the Ascidiæ-larva undergoes after its establishment at the mid-line, the most interesting (after the loss of the axial rod) is the atrophy of one of its chief organs, the mandibular tube. In the Apylomimetic the spinal marrow continues to develop, but in the Ascidiæ the right side shrivels into a small and insignificant nervous ganglion that lies above the mouth and the gill-slits, and is in accord with the extremely slight mental powers of the animal. This degenerate relic of the mandibular tube seems to be quite beyond comparison with the nervous centre of the vertebrates, yet it started from the same structure as the spinal cord of the Apylomimetic. The nerve-organs that had been developed in the fore part of the neural tube are also lost; no trace of them can be found in the adult Ascidiæ. On the other hand, the alimentary canal becomes a most extensive organ. It divides presently into two sections—a tracheal or branched gut that serves for respiration, and a narrower hind or hepatic gut that accomplishes digestion. The branchial or buco-gut of the Ascidiæ is small at first, and opens directly outside only by a couple of lateral slits or gill-slits—a permanent arrangement in the Capitata. The gill-slits are developed in the same way as in the Apylomimetic, but greatly so.

A large gill-cleft, passed like fat work. In the middle line of its upper side we find the hypopharyngeal groove. The mouth or pharynx (the surface) that surrounds the gill-cleft is also

formed in the same way in the Ascidiæ as in the Apylomimetic. The siphon-opening of this peribranchial cavity corresponds to the branchial pore of the Apylomimetic. In the adult Ascidiæ the branchial gut and the heart on its ventral side are almost the only organs that recall the original affinity with the vertebrates.

The further development of the Ascidiæ in detail has no particular interest for us, and we will not go into it. The chief result that we obtain from its embryology is the complete agreement with that of the Apylomimetic in the earliest and most important embryonic stages. They do not begin to diverge until after the mandibular stage and elementary level, and the axial rod with the muscles between the two, have been formed. The Apylomimetic continues to advance, and represents the embryonic forms of the higher vertebrates; the Ascidiæ degenerates more and more, and at last, in its adult condition, has the appearance of a very imperfect myriapod.

If we now look back on all the remarkable features we have circumscribed in the structure and the embryonic development of the Apylomimetic and the Ascidiæ, and compare them with the features of man's embryonic development which we have previously studied, it will be clear that I have not exaggerated the importance of these very interesting animals. It is evident that the Apylomimetic from the vertebrate side and the Ascidiæ from the invertebrate form the bridge by which we can span the deep gulf that separates the two great divisions of the animal kingdom. The radical agreement of the lancelet and the sea-squirt in the first and most important stages of development shows something more than their affinity and their proximity in classification. It shows a close blood-relationship and their origin in the same time. Let us then throw considerable light on the other roots of man's genealogical tree.

## CHAPTER XVIII.

## DURATION OF THE HISTORY OF OUR STEM

Our comparative investigation of the anatomy and embryology of the Amphibia and Aves has given us invaluable assistance. We have, in the first place, bridged the wide gulf that has existed up to the present between the Vertebrates and Invertebrates; and, in the second place, we have discovered in the embryology of the Amphibia a number of ancient evolutionary stages that have long since disappeared from human embryology, and have been lost, in virtue of the law of arrested heredity. The chief of these stages are the spherical blastula (in its simplest primary form) and the succeeding archigastria, the pure, original form of the gastrula which the Amphibia has preserved to this day, and which we find in the same form in a number of vertebrates of various classes. Not less important are the later embryonic forms of the coelomula, the cleidota, etc.

Thus the embryology of the Amphibia and the Aves has so much increased our knowledge of their systematical than, although our empirical information is still very incomplete, there is now no doubt of any great consequence in it. We may now, therefore, approach our proper task, and reconstruct the phylogeny of man in his chief lines with the aid of this evidence of comparative anatomy and ontogeny. In this the reader will soon see the immense importance of the direct application of the Biogeographic law. But before we enter upon the work, it will be useful to make a few general observations that are necessary to understand the processes aright.

We must say a few words with regard to the period in which the human race was evolved from the animal kingdom. The first thought that occurs to me is

between the duration of man's ontogeny and phylogeny. The individual needs only nine months for his complete development, from the formation of the ovum to the moment when he leaves the maternal womb. The human embryo rises to 'wholly organic in the belief' stage of

sixty weeks (as a rule, six days). In many other mammals the time of the embryonic development is much the same as in man—for instance, in the cow. In the horse and ass it takes a little longer, forty-three or forty-five weeks, in the camel, thirteen months. In the largest mammals, the embryo needs a much longer period for its development in the womb—a year and a half in the rhinoceros, and thirty weeks in the elephant. In these cases pregnancy lasts twice as long as in the case of man, or one and three-quarter years. In the smaller mammals the embryonic period is much shorter. The smallest mammals, the shrews, develop in three weeks; bats in four weeks, rats and dormice in five weeks, the dog in nine, the pig in seventeen, the sheep in twenty-one, and the goat in thirty-six. Birds develop still more quickly. The chick only needs, in normal circumstances, three weeks for its full development. The duck needs twenty-five days, the turkey twenty-seven, the guinea-fowl forty-one, the stork forty-two, and the ostrich forty-five. The smallest bird, the humming-bird, leaves the egg after twelve days. Hence the duration of individual development within the fetal membranes is, in the mammals and birds, clearly related to the absolute size of the body of the animal in question. But size is not the only determining factor. There are a number of other circumstances that have an influence on the period of embryonic development. In the Amphibia the earliest and most important embryonic processes take place so rapidly that the blastula is formed in four hours, the gastrula in six, and the typical vertebrate form in twenty-four.

In every case the duration of ontogeny

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plus it with the enormous period that has been necessary for phylogeny, or the gradual development of the ancestral series. This period is not measured by years or centuries, but by thousands and millions of years. Many millions of years had to pass before the most advanced

water, now, was required, step by step, from his natural water-holding capacities. The opponents of evolution, who declare that the greatest advancement of the human race was over cultural forces, and especially from a materialist viewpoint, or an irrational source, forget that the same religious minds also believe in the agency of God in the further development of every human being. Back at least, at the first stages, progress appears to be the free work of God, developing in the womb, passing through the same series of improvements that our cultural agencies undergo in the course of culture or art.

It is impossible to determine even approximately, in hundreds, or even thousands of years, the real and absolute duration of the prehistoric period. But for some time now we have, through the research of geologists, been in a position to assign the relative length of the various periods of the organic history of the earth. The method lies in determining the relative lengths of the geological periods, as found in the remains of the successive eras—the groups that have been derived on the basis of the one or at least a few from the next or other deposited there. These represent layers of limestone, sandstone, shale, clay, etc., which make up the greater part of the rocks, and are often greatly disturbed by them, giving us a standard for comparing the relative length of the various periods.

To make the point quite clear, I will say a word about the evolution of the earth in general, and pass on briefly the chief features of the story. In the first place, we consider the principle that all the great organic life began to exist at a definite period. This however, no longer depends by any competent geologist on dogma. The organic history of the earth could not commence until it was possible to exist on our planet in full condition. Every organism exists, needs fluid water as a condition of existence, and requires a certain quantity of it. Our own body, when fully formed, contains thirty to forty per cent of water in its tissues, and only thirty to forty per cent of solid matter. There is more water stored in the body of the adult, and still more in the embryo. In the earlier stages of development the human fetus contains more than thirty per cent of water, and not less than half of water in the liquid amniotic sac.

Oppositely certain evidence, the body contains on the average of more than thirty per cent, of air water, air has not one per cent of solid matter. So opposite are man or dolphin to human embryo or fetus. We come on like!

But that water, on which the continuity of life primarily depends, could not exist in any form until the temperature of the surface of the surrounding sphere had risen to a certain point. Up to that time it remained in the form of snow. But since as the hot sun comes round in summer from the prototype of winter, it begins its geological action, and has continued down to the present day to modify the solid crust of the earth. The final outcome of this unceasing action of the sun—wearing down and dissolving the rocks in the form of rain, flood, wave, and ice, as running streams or building up—is the formation of land. An Huxley says in his celebrated Lecture on the Course of Philosophy as it Operates Nowhere, the chief document in the pale history of our world is mud; the operation of the history of pale ages—mud, itself has a pale history the formation of mud.

So I have said, it is possible to form an approximate idea of the relative age of the various eras by comparing those of different parts of the world's surface. Geologists have long been agreed that there is a definite geological sequence of the different eras. The northern upper hemisphere has been compared to successive periods in the organic history of the earth, as there they were deposited in the form of sand or the leaves of the sea. The sand was gradually converted into stone. This was lifted out of the water, passing in successive as the earth's surface, and formed the continents. As a rule, the five great continents are distinguished in the organic history of the earth corresponding to the larger and smaller groups of the successive eras. The larger periods are then subdivided into a series of smaller ones, which usually number from twelve to fifteen. The comparative thicknesses of the groups of strata enables us to make an approximate judgment of the relative length of these various periods of time. The question is, is it true? Is a tertiary a division of a certain thickness between two folds in the strata on the average therefore, a lower Lias, but thick sand bed, three feet, four feet, etc.? Different places give different answers, but they

## DURATION OF THE HISTORY OF OUR STEM

the thickness or size of the strata we can only make conclusions as to the relative length of the period.

The first and oldest of the four or five chief divisions of the organic history of the earth is called the primordial, archaic, or archæozoic period. If we compute the total average thickness of the sedimentary strata at about 130,000 feet, this foot

( $\frac{1}{2}$  in.) indicates—possibly 9,500. Of late years the thickness of the archæozoic rocks has been put at 90,000 feet.

The primordial period falls into three subordinate sections—the Laurentian, Hæringian, and Cambrian, corresponding to the three chief groups of rock which comprise the archæic formation. The successive period during which this

### SYNOPSIS OF THE PALEONTOLOGICAL FORMATIONS, OR THE FOSSILIFEROUS STRATA OF THE CRUST

<b>V Anthropicæ</b> Group of strata (Archæozoic)	<b>XIV Eocene</b> Group of strata (Tertiary)	<b>V. Devonian</b> Group of strata	<b>Lower Cambrian</b> Group of strata (Archaean)
<b>III. Arthropoda</b> Group of strata (Archæozoic)	<b>XIII. Mammalia</b> Group of strata (Tertiary)	<b>IV. Brachiopoda</b> Group of strata (Devonian)	<b>Lower Cambrian</b> Group of strata (Archaean)
<b>II. Trilobites</b> Group of strata (Archæozoic)	<b>XII. Primates</b> Group of strata (Tertiary)	<b>III. Crustacea</b> Group of strata (Devonian)	<b>Upper Cambrian</b> Group of strata (Archaean)
<b>I. Bryozoa</b> Group of strata (Archæozoic)	<b>XI. Primates</b> Group of strata (Tertiary)	<b>II. Brachiopoda</b> Group of strata (Devonian)	<b>Upper Cambrian</b> Group of strata (Archaean)
<b>Subtotal</b> Group of strata (Archæozoic)	<b>X. Primates</b> Group of strata (Tertiary)	<b>I. Crustacea</b> Group of strata (Devonian)	<b>Upper Cambrian</b> Group of strata (Archaean)
<b>Total</b> Group of strata (Archæozoic)	<b>IX. Primates</b> Group of strata (Tertiary)	<b>Lower Cambrian</b> Group of strata (Archaean)	<b>Upper Cambrian</b> Group of strata (Archaean)

period comprises 70,000 feet, or the greater part of the whole. For this and other reasons we may at once conclude that the corresponding primordial or archæozoic period must have been in itself much longer than the whole of the remaining periods together, from its close to the present day. It was probably much longer than the figure I have quoted

when writing in the primitive work, probably comprising more than 90,000,000 years. At the commencement of it the simplest and simplest organisms were formed by spontaneous generation—the Monera, with which the history of life on our planet opened. From these were first developed unicellular organisms of the simplest character, the Protophytæ

and Protozoa (protozoans, monads, rhizopods, infusoria, and other Protozoa). During this period the whole of the herpetofauna known at the time was also created from the vertebrate progenitors. We can deduce this from the fact that we already find remains of the earliest Ichthyes (fishes) and Ganozoa (corals) very early in the following Silurian period. These are much more advanced and much larger than the brachiopods, the cephalopods, and the numerous smaller vertebrates, related to the Ammonoidea, that must have lived at this time. The source of the information concerning all the groups may now have preceded them.

The pre-ordovician age is followed by a high marine division, the Silurian or Ordovician age. It is divided into four long periods, the Wenlock, Darriwilian, Caradocian, and Pridolian. The Silurian zone is particularly interesting because they comprise the first land fauna of vertebrates—fishes and snakes of Sheldrick's (Sheldrake's) in the lower, and Cymene (Pembrey's) in the upper Silurian. During the Caradocian period the "old and primitive" had passed, during the Caradocian period very depressions the new and modern forms, old as well as new, had begun to represent, in the Pridolian (or the Dyfiach St. Genn), the new red conditions, the Barbian (Upper Silurian Intervale), and the Keppler-Helderland stage were formed. The outline of these stages is put in order as follows. In any case the primitive, old, taken as a whole, was too sheltered from the protecting mud banks longer than the subsequent periods. The areas that were depressed during this primary epoch number a large number of faults, while the land-shore species there are a great many varieties, and the fishes are few. There were so many fishes, especially primitive fishes of the stony and rocky fishes, during the Caradocian and Pridolian periods, that we may designate the whole paleozoic period as "the age of fishes." During the paleozoic period between Cambrian and the Ordovician (Silurian) are of great importance.

During this period some of the fishes began to adapt themselves to living on land, and to grow also in the size of the bodies. We find in the Caradocian and land-hatched remains of Devonian fishes, in the Silurian, the following remains. These include

belonging to vertebrates in the Pridolian epoch. Through the ages of it we find the first Ammonoidea, the remains of the three higher classes of Vertebrates. There are found the corals; the first to be discovered was the *Polyptychites*, from the sand of Bremen. The rest of the earliest Ammonoidea, among which must have been the common ancestor of the cephalopods, brachiopods, and mammals, is yet back towards the close of the paleozoic age by the discovery of *Gigas cephalites* remains. The sources of our men during this period were as far represented by trees living then by diatoms and fungi, and finally by the earliest Ammonoidea, or the Pridolian.

The third chief season of the organic history of the earth is the Mesozoic or Secondary period. This again is subdivided into three divisions, Triassic, Jurassic, and Cretaceous. The third group of the rocks that were deposited in this period, from the beginning of the Triassic to the end of the Cretaceous period, is altogether about a long time, or not half as much as the paleozoic deposits. During this period there was a very broad and extended development in all branches of the animal kingdom. There were especially a number of new and interesting forms evolved in the vertebrate class. Many fishes (Teleostei) made their first appearance. Reptiles are found in extraordinary variety and number; the earliest chord-mammals (Archaeoceras), the well-known *Diplocaulus*, and the *Brachiosaurus* (Archaeosaurus) are the most remarkable and best known of them. On account of the predominance of the reptiles in the ground is called "the age of reptiles." But the herbivores were also evolved during this period. They conspicuously originated from more advanced of the fossil like reptiles. This is proved by the embryological identity of the birds and reptiles, and their common ancestry, and, among other facts, from the circumstance that in this period there were birds with teeth in their jaws and with tails like lizards (Archaeopteryx, Oviraptor).

Finally, the most advanced and the most important class of the vertebrates, the mammals, made their appearance during the secondary period. The first few groups of them were found in the lower Triassic rocks, from which appear and disappear, the last remaining as such a short time

In the Jura-nic, and more in the Cenozoic. All the mammals remain that we have from this period belong to the lower primates and mammals; among these were most certainly the ancestors of the human race. On the other hand, we have not found a single indubitable fossil of any higher mammal in pliocene; in the whole of this period. This absence of the mammals, which includes man, was not developed until later, towards the close of this or in the following period.

The fourth section of the geological history of the earth, the Tertiary, or Cenozoic, was much shorter than the preceding. The series that were deposited during this period have a collective thickness of only about 3,000 feet. It is subdivided into four sections—the Eocene, Oligocene, Miocene, and Pliocene. During these periods there was a very rapid development of higher plants and animal forms, the flora and fauna of our planet approached nearer and nearer to the situation that they bear today. In particular, the most advanced class, the mammals, began to predominate. Hence the Tertiary period may be called "the age of mammals." The highest section of this class, the pliocene, now made their appearance, so this group the human race belongs. The first appearance of man, or, to be more precise, the development of man from some closely related group of apes, probably falls in either the miocene or the pliocene period, the middle of the last section of the Tertiary period. Others believe that man—nearly so-called—was endowed with speech—was not evolved from the non-speaking apes (Pitheciomorphæ) until the following, the anthropoid, age.

In this fifth and last section of the geological history of the earth we have the development and dispersion of various races of men, and so it is called the Anthropoid, as well as the Pleistocene period. In the imperfect condition of paleontological and ethnographical science we cannot as yet give a decided answer to the question whether the evolution of the human race from some extinct apes or lower tool-giving at the beginning of this or towards the middle or the end of the Tertiary period. However, this much is certain: the development of primitive tools in the anthropoid age, and this in spite of the indigence of the last period of the whole history of life. When we

remember this, it seems ridiculous to restrict the word "history" to the civilized period. If we divide into a hundred equal parts the whole period of the history of life, from the spontaneous generation of the first bacteria to the present day, and if we then represent the relative duration of the five chief sections of time, as calculated from the average thicknesses of the mass they contain, no approximation of this, we get something like the following relation:

I. Archaean or eonozoic (pre-embryonic) age	31	4
II. Palaeozoic or palaeozoic embryonic age	15	1
III. Mesozoic or embryo (embryonic) age	11	1
IV. Cenozoic or embryo (embryonic) age	8	1
V. Anthropoid or anthropo-embryonic (paleozoic) age	3	1

In any case, the "historical period" is an independent spanner associated with the real length of the preceding ages. In truth there was no question of human culture in our planet. In the last Cenozoic or Tertiary period, in which the first mammals or higher mammals appear, probably amounts to half over to one per cent. of the whole embryonic age.

Before we approach our proper task, and with the aid of our encyclopedic knowledge and the biological law, follow step by step the palaeo-embryological development of our animal kingdom, but in a sense for a moment at another, and apparently quite remote, horizon of science, a general consideration of which will help us in the solving of a difficult problem, I mean the science of comparative physiology. Since Darwin gave new life to biology by his theory of selection, and raised the question of evolution in all fields, it has often been pointed out that there is a remarkable analogy between the development of languages and the evolution of species. The comparison is perfectly just and very instructive. We cannot hardly find a better analogy when we are dealing with some of the difficult and elusive features of the evolution of species. In both cases we find the action of the same natural law.

All physiologists of every importance in their science now agree that all living languages have been gradually evolved from very rudimentary beginnings. The

tion that appears in a grid of the grades of life held by differentiated entities. Atty 60, years ago we now generally admitted, and only supported by linguists and others who think as natural development continues. Speech has been developed discontinuously, with no regularity, the Aryans and Greeks, and also the Americans of the brain. Hence it will be quite natural to find in the evolution and classification of languages the same features as in the evolution and classification of organic species. The various groups of languages that are distributed in physiology as primitive, degenerated, pure, and daughter languages, etc., correspond entirely to their development in the different categories which we classify as living, and human; as prime, classic, ethnic, human genera, species, and varieties. The relation of these groups, partly according to their importance in the general system, is just the same as that above, and the structure below, & the same thing is true.

When we follow the categories of this type, we follow the formation of the various languages that have been developed from the common root of the ancient Indo-Germanic tongue, we get a very clear idea of their phylogeny. We shall see at the same time how analogous this is to the development of the various groups of vertebrates that have arisen from the common parents of the primitive vertebrate. The ancient Indo-European representatives divided three ages into primitive, the Indo-Germanic and the Aryo-Hellenic. The Indo-Germanic then branched into the Indian-Germanic and the ancient Indo-Latin. The Aryo-Hellenic into the ancient Aryan and the ancient Greek-Roman. If we will follow the genealogies one of these four Indo-European tongues, we find that the ancient German divides into three branches, the Saxon, the East, the Gothic, and the German. From the ancient Germans were the High German and Low German, to the latter belong the Frisian, Saxon, and modern Low-German dialects. The eastern Germans divided first into a Baltic and a Slav language. The Baltic gave rise to the Latvian, Lithuanian, and old-Pomeranian varieties, the Sow to the Slavonic and Wend-Silesian in the north-east, and to the Polish and Czech in the west.

We find an equally parallel branching off the two chief stems when we look to

the other division of the Indo-Germanic language. The German-Roman divided into the Thuringian (Alanus-Graecia) and the Indo-Celtic. From the latter arose the divergent branches of the Baltic (Lithuanian and Latvian) in the south, and the Celtic in the north, from the latter have been developed all the Bretons (upwards Breton, western French, and Irish), and Gallo-Briton. The ancient Aryans gave rise to the various German and Latin languages.

The "comparative anatomy" and analysis of languages admirably illustrates the phylogeny of "races". It is clear that in structure and development the primitive languages, mother and derivative languages, and varieties correspond exactly to the classes, orders, families and species of the animal world. In such cases the "races" are more in phylogeny. As we have here even rapid cross-comparisons and interagency, and thus hybridization, that all this and living vertebrates illustrate. But it is necessary, as the comparison is made of dead and living Indo-Germanic tongues proves beyond question that they are all manifestations of one primitive language. This view of their origin is now accepted by all the chief philologists who have worked in this branch and are unprejudiced.

But the point on which I desire particularly to draw the reader's attention is the comparison of the Indo-Germanic language with the members of the systematic family in that one race never passes direct development in all cultural processes, nor does it do so with living. This applies as a very普遍, and our opponents often make use of the expression when it proves to be for the purpose of attacking polytheism generally. When, for instance, we say that man develops from the ape, this shows the former, and the latter shows the developed, many people suppose that we are thinking of the living species, of those orders of mammals that they had called to our ancestors. Our opponents, that find this idea an abomination, wish to prove that they are incapable; or they call us, by way of physiologically experiment, to have a language like a horse, a horse like a goat, and a goat like a pony! This is absurd in children, and the idea it represents. All these living forms have changed more or less from the original form; none of them could compare the

more posterior than the ones that really possessed them, thousands of years ago.

It is certain that man has descended from more ancient mammals; and we should just as certainly class this in the order of ages if we had it before us. It is equally certain that this primitive species evolved in turn from an even more ancient mammal, and this from an even more ancient. But it is just as clear that all these ancient ancestral forms can only be claimed as belonging to the living order of mammals in virtue of their ancient internal structures and their resemblance to the distinctive mammalian characteristics of each order. In external appearance in the characteristics of the genus or species, they would differ more or less, perhaps very considerably, from all living representatives of these orders. It is a natural and natural procedure in phylogenetic development that the older forms should differ, and in their specific peculiarities, have been apart for some time. The fossilized short apparent return to stages among the living species are more or less — perhaps very substantially — different from them. Hence in our phylogenetic inquiry and in the comparative study of the living, divergent descendants, there not only is a question of determining the greater or less resemblance of the fauna from the ancestral forms. Nor is a single one of the older mammals has continued unchanged down to our time.

We find just the same thing in comparing the various dead and living languages that have descended from a common primitive tongue. If we examine the genealogical tree of the Indo-European languages in this light, we see at once that all the older or parent tongues, of which we regard the living varieties of the Aryan as divergent daughter or grand-daughter languages, have been extinct for some time. The Aryo-Romanic and the Slave-Germanic tongues have completely disappeared; so also the Persian, the Greek-Roman, the Slave-Latin, and the ancient Germanic. Even these daughters and grand-daughters have been lost; all the living Indo-Germanic languages are only related in the sense that they are divergent descendants of common ancestors. Some three have descended now, and now less, were the original ones.

This easily demonstrates that there is no conflict between man and the monkeys as of the origin of the vertebrate species. Phylogenetic

comparative physiology here yields a strong support to phylogenetic comparative zoology. But this we can obtain more direct evidence than the other, as the paleontological material of physiology—the old craniometric of the subject—has preserved much better than the paleontological material of zoology, the anatomical bones and implants of vertebrates.

We may, however, take man's phylogenetic tree not only up to the living mammals, but much further — to the amphibia, as the shark-like primitive form, and, in fact, to the simplest vertebrates that clearly manifested the Amphibia. But this must not be understood in the sense that the existing Amphibia, or the sharks or amphibia of today, can give us any idea of the external appearance of these remote ancestors. This can most easily be thought that the Amphibia — any armed shark, or any living species of amphibia, is a real ancestral form of the higher vertebrates and man. The statement can only reasonably mean that the living forms I have referred to are sufficient forms that are much more closely related to the earliest man-forms, and have retained his characteristics much longer, than any other animals we know. They are old as these in respect to their phylogenetic internal structure that we should put them at the early days with the ancient forms if we had them before us. But the direct descendants of these earlier forms have remained unchanged. Hence we must entirely abandon the idea of finding direct ancestors of the human race in those characteristic animals from among the living genera of animals. The constant and distinctive features that will connect living forms more or less closely with the earliest common man-forms lie in the internal structures, not the external appearance. The latter has been much modified by adaptation. The former has been more or less preserved by heredity.

Comparative anatomy and embryology beyond question that man is a high vertebrate, and, therefore, man's spinal column must be compared with that of the other Vertebrates, which spring from a woman and with him. But we have also many important grounds in comparative anatomy and embryology for accepting a common origin for all the Vertebrates. If the general theory of

which is evident, all the *Vertebrates*, including man, come from a single common ancestor, a long-extinct "Primiti<sup>v</sup>le *Vertebrate*." Hence the phylogenetic line of the *Vertebrates* is at the same time the line of the human race.

Our task, therefore, of conserving man's generality becomes the larger also of discovering the genealogy of the more numerous others. As we are here from the comparative anatomy and embryology of the *Aquaticus* and the *Auricula*, this is at least connected with the genealogical tree of the *Invertebrates* (doubtless with that of the *Vertebrates*), but has no direct connection with the independent stems of the *Arthropods*, *Molluscs*, and *Vertebrates*. If we do these follow and connect the through various stages down to the lowest worms, we never lose fidelity to the *Genotype*, that most last-lasting form that gives the clearest possible picture of an animal with the permanent parts. The *Genotype* could not originate from the simple multicellular vehicle, the *Sphaerozoa* and this is how such have been evolved from the lower units of multicellular animals, to which we give the name of *Prokaryotes*. We have already considered the three main groups primitive types of them, the *cellular*, *Amoeboid*, which is extremely important when compared with the higher types. With this we reach the bottom of the root that to which we are to apply our hypothesis here, and by which we may deduce the various complex forms of the *inorganic* flora. The simplest types of the young ones and the quiescent condition in which (as sleep-well or cycles) every living being keeps its existence firmly, so as showing that the surface structures of the bodies are not wholly destroyed with.

But the further question now arises—Whence come those first materials with which the history of life begins at the commencement of the *Living* species? There is only one answer to this. The most minute organic parts are only here been evolved from the *inorganic* hypothesis we know, the *Minerals*. These are the simplest living things that we can conceive. Their whole body is nothing but a particle of mineral, a granule of *Primiti<sup>v</sup>le mineral*, disintegrating of itself all the essential vital functions that form the material basis of life. Thus we come to the last or, if you prefer, the first, question in connection with evolution—the question of the origin of the *Minerals*.

This is the real question of the origin of life, or of spontaneous generation.

We have another point now remaining to go further in the Chapter into the question of spontaneous generation. For this I must refer the reader to the Spanish chapter of the *History of Creation*, and again by to the second book of the *General Philosophy*, or to the essay on "The Minerals and Spontaneous Generation" by my Author of the *Minerals and other Products*. I have given there fully my own view of this important question. The famous German Naturalist *Hegel* afterwards (1846) developed the same idea. I will only say a few words here about this strange question of the origin of life, in so far as our main subject, organic evolution in general, is influenced by it. Spontaneous generation, in the definite and restricted sense in which I understand it, and when there is a necessary hypothesis in explaining the origin of life, refers solely to the evolution of the *Minerals*, from inorganic organic components. When living things develop their first appearance in our planet, the very simplest, most perfect compound of surfaces that we call plants, a bird, or the most complex combination of road and sea, must have been formed in a finely rounded egg from inorganic organic components. The first *Minerals* were formed in the sea by spontaneous generation, as crystals were formed in the mother water. Our demand for a knowledge of organic crystals is to suppose this. If we believe that the whole biological history of the earth has proceeded in mechanical principles we have no interest in a *Creator*, and that the history of life also has been determined by the laws mentioned above. If we see that there is no need to admit creative action to explain the origin of the various groups of organisms; it is utterly furnished to remove such creative action in dealing with the first appearance of organic life on the earth.

This much-disputed question of "spontaneous generation" seems as though various people have associated with the term a mass of very different, and often very absurd, ideas, and have attempted to solve the difficulty by the easiest expedient. The real doctrine of the spontaneous generation of life seems hardly to remain by supporters.

"The theory of the 'spontaneous generation' of living matter is a theory which has been exploded by the most recent researches."

Every experiment that has a negative result only proves that no organism has been formed out of inorganic matter in the conditions—highly artificial conditions—we have established. On the other hand, it would be exceedingly difficult to prove the theory by way of experiment; and even if Moera were still formed daily by spontaneous generation (which is quite possible), it would be very difficult, if not impossible, to find a solid proof of it. Those who will not admit the spontaneous generation of the firm living things in our sense must have recourse to a supernatural miracle; and this is, as a matter of fact, the desperate resource to which our "exact" scientists resorted.

A famous English physicist, Lord Kelvin (then Sir W. Thomson), attempted to dispense with the hypothesis of spontaneous generation by assuming that the organic inhabitants of the earth were descended from germs that came from the inhabitants of other planets, and that chance to fall on our planet on fragments of their original home, or *Mutterland*. This hypothesis found many supporters, among others the distinguished German physicist, Helmholtz. However, it was refuted in 1872 by the able physician, Friedrich Zeliner, of Leipzig, in his work,

*On the Nature of Chemot.* He showed clearly how unscientific this hypothesis is; firstly in point of logic, and secondly in point of scientific content. At the same time he pointed out that our hypothesis of spontaneous generation is "a necessary condition for understanding nature according to the law of causality."

I suspect that we must call in the aid of the hypothesis only as regards the Moera, the structureless "organisms without organs." Every complex organism must have been evolved from some lower organism. We must not assume the spontaneous generation of even the simplest cell, for this itself consists of at least two parts—the internal, finer nuclear substance, and the external, coarser cellular substance or the protoplasm of the cell-body. These two parts must have been formed by differentiation from the indistinct plasm of a moneron, or a cytozoa. For this reason the natural history of the Moera is of great interest: here alone can we find the means to overcome the chief difficulty of the problem of spontaneous generation. The actual living Moera are specimens of such organisms or structureless organisms, as they must have been formed by spontaneous generation at the commencement of the history of life.

## CHAPTER XIX.

### OUR PROTIST ANCESTORS

With the guidance of the biogenetic law—*the basis of the evidence we*

*are using*—  
Physiognomy

*as a whole is an inductive*—  
the totality of the biological processes in  
the life of plants, animals, and men we  
have gathered a confident inductive idea  
that the whole organic population of our  
planet has been moulded on a harmonious  
law of evolution. All the interesting

phenomena that we meet in ontogeny and phylogeny, comparative anatomy and cytology, the distribution and habits of organisms—all the important general laws that we abstract from the phenomena of these sciences, and combine in harmonious unity—are the broad bases of our great biological induction.

But when we come to the application of this law, and seek to determine with its aid the origin of the various species of organisms, we are compelled to frame

systems that have essentially a determinate character, and are therefore from the general law to particular laws. The three special determinants are just as well defined and determined by the rigorous laws of logic as the individual conditions in which the whole theory of evolution is built. The doctrine of the natural history of the human race is a special deduction of this kind, and follows with logical necessity from the general biological law of evolution.

I must point out at once, however, that the certainty of these evolutionary hypotheses, which rest on this special deduction, is not always a equally strong. Some of these influences are more far and deeper, in the sense of being of deeper origin, than others; and the importance of the respective stages degrees of certainty he provided as those in any case, a closer approach between the absolute certainty of the general (natural) theory of change and the relative certainty of special (determinate) evolutionary hypotheses. We can never determine the whole causal series of an organism with the same confidence with which we hold the general theory of evolution as the only systematic representation of organic modifications. The greater influence of man here is doubt will always be seen in his assumptions and by probability. This is quite natural. The evidence on which we build is imperfect, and always will be imperfect, just as it is impossible perfectly.

The basis of our determinate paleontology, is amazingly incomplete. We know that all the fossils we discovered are only a negligible fraction of the plants and animals that have lived on our planet. For on one single species that has been preserved to us in the rocks there are probably thousands, perhaps thousands, of different species that have left no trace behind them. This extreme and very unfortunate incompleteness of the paleontological evidence, which cannot be remedied in any other, is easily explained. It is obviously our task in the construction of the foundation of evolution. It is also due in part to the incompleteness of our knowledge in this branch. It must be borne in mind that the great majority of the scientific results that concern the rest of the earth have not yet been applied. We have only a few specimens of the innumerable fossils that are buried in the the remote ranges of Asia and Africa.

Only a part of Europe and North America have been investigated recently. The whole of the globe known to us certainly do not amount to a hundredth part of the remains that are surely buried in the rest of the world. We may, therefore, look forward to a rich harvest in the future as regards this science. However, our paleontological evidence will prove soon that I have fully explained in the chapter chapter of the "History of Civilization" always be defective.

The second class consists of evidence, however, is not less important. It is the most important source of all the special paleontology; but it has great defects, and this is, in the first place, above all, clearly distinguishable from paleontology and comparative anatomy. It is most often longer than the laws of inheritance and differential heredity often make the original source of development almost unnecessary. The recognition of phylogeny by analogy is only fairly complete in a few cases, and is never wholly complete. As a rule, it is precisely the earliest and most important cases that escape their most from a posterior and secondary. The earlier history was, however, based on analogies that were not exact enough, and so has a poor foundation. The struggle for existence has had just as profound an effect on the truly developing and still immature young forms as on the adult forms. Hence in the paleontology of the higher animals, especially, relationships of stock and related by comparison, as in biology, as a rule, only a faded and much altered picture of the original evolution of the animal's nature. We can only draw one lesson from the comparative forms, to the descendants with the greatest caution and circumspection. Moreover, the comparative development itself has only been fully studied in a few species.

Finally, the third and most valuable class of evidence, which give a certainty, is also, unfortunately, very defective; the single except that the whole of the living species of animals are a mere fraction of the total population that has lived on our planet since the beginning of life. We may confidently put the total number of these at more than a million species. The number of animals whose generation has been studied up to the present is comparative anatomy is probably very small. Very again, future research will yield favorable results,

But, for the present, in view of this general introduction of our chief sources of evidence, we must naturally be compelled to lay too much stress in biology phylogeny on the particular animals we have studied, or regard all the various stages of development with equal interest.

In my first efforts to construct the story of man's ancestry I drew up a list of, at first ten, afterwards twenty to thirty, forms, that may be regarded more or less certainly as animal ancestors of the human race, or as stages that at a time mark off the chief vicissitudes in the long story of evolution from the unicellular organization up to man. Of these twenty to thirty stages, ten to twelve belong to the older group of the Invertebrates, and eighteen to twenty to the younger division of the Vertebrates.

In approaching, now, the different task of establishing the evolutionary sequence of these thirty ancestors of humanity, based on the increasing size and increasing ability to live that marks the earlier stages of the earth's history, we must undoubtedly look for the first in our thoughts among the wonderful organisms that we call the Monera; they are the simplest organisms known to us—in fact, the simplest we can conceive. They have had to invent a whole variety of a simple particle or globule of structureless plasma of protoplasm. The development of the last few decades has led us to believe with increasing certitude that whether a material body exhibits the vital processes of nutrition, reproduction, voluntary movement, and respiration, we have the action of a nervous substance composed of the chemical group of the allometabolites, that plasma (or protoplasm) is the material basis of all vital functions. Whether we ascribed the function, to the nervous system, or the direct action of the material vital matter, or whether we take matter and force to be distinct things at the ultimate stage, it is certain that we have not as yet found any living organism in which the exercise of the vital functions is not inseparably bound up with protoplasm.

The soft silvery plasma of the body of the moneran is generally called "protoplasm," and identified with the cellular mass of the ordinary plant and animal cells that we meet, to be contrasted

with the plasma of the crystals and the protoplasm of the cells. This distinction is of the utmost importance for the purpose of evolution. As I have often said, we must recognize two different stages of development in these "simplest organisms," or protoplasm ("builders"), that represent the ultimate units of organic individuality. The surface and lower stage are the unicellular system, the body of which consists of only one kind of chemically similar—the homogeneous plasma or "homogeneous matter." The later and higher stage are the nucleated cells, on which we find a differentiation of the organic plasma into two different forms—two different substances—the cytoplasm of the nucleus and the cytoplasm of the body of the cell (cf. pp. 27 and 41).

The Monera are primitive; these were the earliest forms of self-continuous plasma. However certainly we conceive it with our most refined reagents and most powerful microscopes,

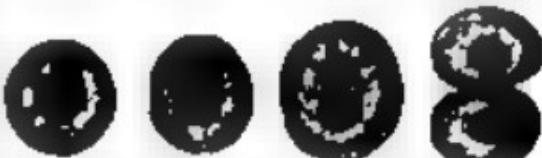


FIG. 4.—Diagrammatic Ideas of Three Different Types of Cells. A diagrammatic representation of three stages of cellular evolution. The first shows a simple cell; the second shows a cell with a nucleus; the third shows a cell with a large nucleus and other organelles.

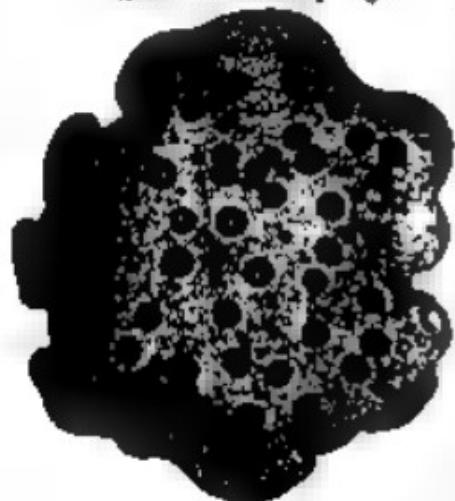
we can find no definite parts or features peculiar to it. Hence, the Monera are literally negative evolved organisms; in fact, from the philosophic point of view they are not organisms at all, since they have no organs. They can only be called organisms on the mere fact that they are capable of the vital functions of nutrition, reproduction, respiration, and movement. If we care to try to imagine the simplest possible organisms, we should form something like the moneran.

The Monera that we find today in various forms fall into two groups according to the nature of their nutrition—the Phyto-moners and the Zoo-moners. From the physiological point of view, the former are the simplest specimens of the plant (protoplasm's) kingdom, and the latter of the animal (force) world. The Phyto-moners, especially in their simplest form, the Chrysophytes (Chrysophyton or Chrysophytes), are the most primitive and the

## OUR PROTIST ANCESTORS

oldest of living organisms. The typical genus *Chrysococcus* (Fig. 226) is represented by several fresh-water species, and when forms a very delicate bluish-green deposit upon mud and wood in ponds and ditches.

Wafts of round, light green particles, about  $\frac{1}{10}$  in. in diameter, of an inch in diameter. The whole life of these homogeneous globules of plasma consists of simple growth and reproduction by cleavage. When the tiny particle has reached a certain size by the continuous intake of inorganic matter, it divides itself in half, by a constriction middly. The two daughter cells formed immediately begin



*Chrysococcus*

similar vital process. It is the same with the brown *Proctostylos peruvianus* (formerly called the *Proctostylos marinum*); it forms large masses of floating matter in the Arctic seas. The tiny plasma-globules of this species are of a greenish-brown colour,

the simplest *Chrysococcus*, but we find one in other members of the same family; in *Aethoscapus* (Fig. 227) the overlapping plasma-globules are pinkish-red; in *Glossopeltis* they are retained through several generations, so that the little plasma-globules are enclosed in many layers of membranes.

Next to the Chromalveans come the Bacteria, which have been evolved from them by the remarkable change in nutrition which gives us the simple explanation of the division of plant

the protist kingdom. The Chromalveans build up their plasma directly from inorganic matter; the Bacteria feed on organic matter. Hence, if we logically divide the protist kingdom into plasma-forming Protophytes and plasma-consuming Protists, we must class the Bacteria with the latter; it is quite illogical to describe them—as is still often done—in Solanomyx-erity, and class them with the true fungi. The Bacteria, like the Chromalveans, have no nucleus. As is well known, they play an important part in modern biology as the causes of fermentation and putrefaction, and of tuberculous, typhus, cholera, and other infectious diseases, and as parasites, etc. But we cannot longer fail to deal with those very interesting features; the Bacteria have no relation to man's genealogical tree.

We now turn to consider the amoeboids, Protomycetes, or unucleated Amoeba. I have, in the first volume, pointed out the great importance of the ordinary Amoeba in connection with several exciting questions of general biology. The tiny Protomycetes, which are found both in fresh and salt water, have the more unshapely form and irregular movements of their simple naked body as the real Amoeba, but they differ from them very materially in having no nucleus in their cell-body. The short, blunt, finger-like processes that are thrust out at the surface of the creeping Protomycete serve for getting food as well as for locomotion. They multiply by simple cleavage (Fig. 228).

The next stage is the simple cytodesmosis of the Monera in the genealogy of animalia (all other animals) is the simple cell, or the most rudimentary form of the cell which we find living independently to-day as the Amoeba. The earliest process of inorganic differentiation in the structureless body of the Monera led to the cell into two different substances—the cytoplasm and the cytoplast. The cytoplasm is the inner and firmer part of the cell, the substance of the nucleus. The cytoplast is the outer and softer part, the substance of the body of the cell. By this important differentiation of the plasma into nucleus and cell-body, the

equivalent cell was evolved from the structureless cytoplasm, the nucleated from the unstructured plastid. Thus the first cell to appear on the earth transformed from the Monera by such a differentiation seems to us the only possible view in the present condition of science. We have a direct instance of this earliest process of differentiation to-day in the ontogeny of many of the lower Protists (such as the Gregarines).

The unicellular form that we have in the ovum has already been described as the reproduction of a corresponding unicellular stem-form, and in this we have described the organization of an Amoeba (cf. Chapter VI). The irregularly-charged Amoebae, which we find living independently to-day in our fresh and salt water, in the least definite and the most primitive of all (Fig. 16),

the unripe ova (the protomere that we find in the ovaries of animals) cannot be distinguished from the common Amoebae, we must regard the Amoeba as the primitive form that is represented in the embryonic stage of the amoeboid ovum to-day, in accordance with the biogenetic law. I have already pointed out, to prove of the striking resemblance of the cells that the ova of many of the sponges were formerly regarded as parthenitic Amoebae (Fig. 18). These unicellular organisms like Amoebae were found creeping about inside the body of the sponge, and were thought to be parthenitic. It was afterwards discovered that they were really the young of the sponge from which the embryos were developed. As a result, these sponge-ova are as numerous as many of the Amoebae in size, shape, the character of their nucleus, and arrangement of the pseudopodia, that it is impossible to distinguish them without knowing their subsequent development.

Let us now return to the question of the relation of the egg to some sort of undifferentiated form, especially the answer to the old problem: "Which was first, the hen or the chick?" We can now give a very plain answer to this riddle, with which our opponents have often tried to drive us into a corner. The egg came a long time before the chick. We do not mean, of course, that the egg existed from the first as a bird's egg, but as an indifferent anucleated cell of the simplest character. The egg lived for thousands of years as an independent

unicellular organism, the Amoeba. The egg, in the widest physiological sense of the word, did not take its appearance until the development of the unicellular Protistæ had developed into multicellular animals, and these had undergone sexual differentiation. Even then the egg was first a gastrula-egg, then a platocoel-egg, then a coelocoele-egg, and chondrocoel-egg; later still neurula-egg, then fish-egg, amniote-egg, reptile-egg, and finally bird's egg. The bird's egg we have seen is of itself a highly complicated structure.

I predict, the result of countless evolutionary processes that have taken place of years,

The simple Protophytes, and from these our protozoic ancestors were developed after the morphological point of view both the vegetal and the animal Protists were simple organisms, indi-

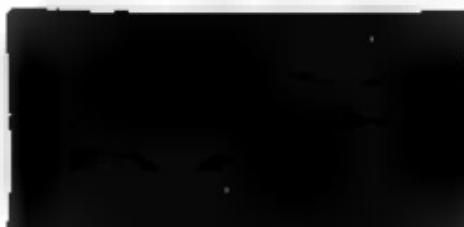


FIG. 18.—A sponge (Diplosomas) — the sort of reproductive cell that was once thought to be parthenitic. This figure shows a young sponge in the form of a small, irregular, lobed mass of protoplasm in the middle, surrounded by a layer of cells, and enclosed in a thin membrane.

viduals of the first order, or plastids. Amoeba's are unicellular organisms — individuals of a higher order — social aggregations of a plurality of cells. The earliest of these, the Amoebae, which represent the third stage in our ontogeny, are very simple associations of protoplasm, individual cells — undifferentiated colonies of social Amoebae or Infusoria. To understand the nature and origin of these protists

we follow step by step the first embryonic products of the stem-cell. In all the Metazoa the first embryonic process is the repeated cleavage of the stem-cell, or first segmentation-cell (Fig. 19). We have already fully considered this process, and found that all the different forms of it may be reduced to one type, the original equal or apical segmentation (cf. Chapter VIII.). In the gametological tree

of the Vertebrates this palingenetic form of segmentation has been preserved in the Amphioxus since, all the other Vertebrates having ontogenetically modified forms of cleavage. In any case, the latter were developed from the former, and so the segmentation of the ovum in the Amphioxus has a great interest for us (cf. Fig. 31). The outcome of this repeated cleavage is the formation of a ciliated

small community of Amoebae arose by the side of these eversible Protozoa, the inter-cells produced by cleavage remaining joined together. The advantages in the struggle for life which these communities had over the isolated cells favoured their formation and their further development. We find plenty of these cell-colonies or communities to-day in both fresh and salt water. They belong to various groups

as - colonial or gregarious amoebae. The small or cilia, formed by invagination of a group of ciliated cells, changes but little, then four (3 & the fifth), and finally a large number of ciliates (Fig. 70).

cluster of cells, composed of homogeneous indistinct cells of the simplest type (Fig. 330). This is called the monera (or mulberry-embryo) on account of its resemblance to a mulberry or blackberry.

It is clear that this results, according to us to-day, the simple structure of the multicellular animal that succeeded the unicellular amoeboid form in the early Laurentian period, in accordance with the biogenetic law, the monera occurs the ancestral form of the Animal, or simple colony of Protista. The first cell-com-

plex of our race that succeeded phylogenetically to the Monera, we have only to follow the further embryonic development of the monera. We then see that the social cells of the round cluster secrete a sort of jelly or a watery fluid inside their globular body, and they themselves rise to the surface of it (Fig. 39 A, B). In this way the solid mulberry-embryo becomes a hollow sphere, the wall of which is composed of a single layer of cells. We call this layer the blastoderm, and the sphere itself the blastula, or embryonic vesicle.

This interesting blastula is very important. The conversion of the monera into a hollow ball proceeds on the same lines originally in the most diverse stems - as, for instance, in many of the siphonophores and corals, the ascidians, many of the echinoderms and molluscs, and in the annelids. Moreover, in the animals in which we do not find a real palingenetic blastula, the defect is clearly due to congenital causes, such as the formation of feed-back and other embryonic aplasia.

With my, therefore, the ontogenetic blastula is the reproductive of a very early phylogenetic stem - all the Metazoa.



In the - Monera, or mulberry-shaped unicellularities to be formed, which laid the early foundation of the higher multicellular body, must have consisted of homogeneous and simple amoeboid cells. The oldest Amoebae lived isolated lives, and even the amoeboid cells that were formed by the segmentation of these unicellular organisms must have continued to live independently for a long time. But gradually

stem-form, which was in the main constructed like the blastula. In many of the lower animals the blastula is not developed

within the fetal membranes, but in the open water. In these cases each blastodermic cell begins at an early stage to thrust out one or more main hair-like processes; the body surface about by the vibratory movement of these hairs or whips (Fig. 29 F).

We still find, both in the fresh water, various kinds of primitive multicellular organisms that substantially the blastula is at

may be n...

" tulip-form—hollow vesicles or gelatinous balls, with a wall composed of a single layer of ciliated homogeneous

There land even among the Protophyta—the familiar Volvocina, formerly classified with the Infusoria. After Hahn, Volvox is found in the ponds in the spring—a small green gelatinous globule, measuring about by means of the action of its lashes, which rise in pairs from the

" after Hahn. Among these also, a herb we find marine plants (floating matter), number of green cells form a simple 6, at the surface of the gelatinous ball; but in this case there are no cilia.

Some of the infusoria of the flagellates (Singer, Alveoplasma, etc.) are similar in structure to these vegetal clusters, but differ in their sexual generation; they form the separate group of the Ciliophora. In September, 1898, I studied the development of one of these graceful animals on the island of Gva-Da, off the shore of Norway (Micrometra pinnata, Figs. 291 and 292). The fully-formed body is a gelatinous ball, with its wall impregnated of the

After reaching maturity the annulation is dissolved. Each cell then loses individual

changes into a creeping mass, afterwards contracts, and closes with a structureless membrane, then looks just like an ordinary

When it has been in this condition for some time the cell divides into two, four, eight, sixteen, thirty-two, and sixty-four cells. These arrange themselves in a round vesicle, about one millimeter in diameter, burst the capsule, and swim about in the sea

blastula, with similar construction, of many of the lower animals, we can confidently deduce from them that there was a very early and long-extinct common stem-form of substantially the same structure—the blastula. We may call it the Blastozoa. Its body consisted, when fully developed, of a simple hollow ball, filled with fluid or structureless jelly, with a wall composed of a single stratum of ciliated cells. There were probably many genera of these, and of these

in plant kingdom also the simple hollow sphere is found to be an elementary form of the multicellular organism. At the surface and below the surface (low depth of 2,000 yards) of the sea the green globules swimming about, with a wall composed of a single layer of chlorophyll-bearing cells. The botanist Schenck gave them the name of Halo-

spora which we find impregnated with the ova-globules of all the Melastom (Fig. 293). As we see, the original, paleogenetic form of the gastrula is a round or oval un-rotted body, the simple cavity of which (the primitive gut) has an aperture at one pole of its axis (the primitive mouth). The wall of the gut consists of the coats of cells, and those are the primary generated layers, the animal skin layer (ectoderm) and vegetal gut-layer (endo-

gen).

A ontogenetic development of strains from the blastula furnishes evidence as to the phylogenetic origin of the Gastraea from the Blastozoa.

In the end this investigation goes so far as to give us a clear idea of the uninvestigated part of the Melastom lies close on the inner or un-investigated part (Fig. 293). In explaining the phylogenetic origin of the gastraea in the light of this ontogenetic process, we may assume that the multi-layered cell-communism of the blastozoa began to take in food more largely at one particular part of its surface. Natural selection would gradually lead to the

formation of a depression or pit at this alimentary spot on the surface of the ball. The depression would grow deeper and deeper. In time the vegetal function of taking in and digesting food would be confined to the cells that lined this hole; the



FIG. 211.—The *Berneytes* *Hypothecariae* embryo, representing about 1000 of the later or older cleavage stages.

other cells would see to the animal functions of locomotion, respiration, and protection. This was the first division of labour among the originally homogeneous cells of the blastula.

The effect, then, of this earliest histological differentiation was to produce two different kinds of cells—nutritive cells in the depression and locomotive cells on the surface outside. But this involved the reversal of the two primary germinal layers—a most important process. When we remember that even man's body, with all its various parts, and the body of all the other higher animals, are built up originally out of these two simple layers, we cannot lay too much stress on the phylogenetic significance of this gastrulation. In the simple primitive gut or gastric cavity of the gastrula and its rudimentary mouth we have the first real organ of the animal frame in the morphological sense; all the other organs have developed afterwards from them. In reality, the whole body of the gastrula is merely a "primitive gut." I have shown already (Chapters VIII. and IX.) that the two-layered embryos of all the Metazoa can be reduced to this typical gastrula. This important fact justifies me in concluding, in accordance with the biogeographic

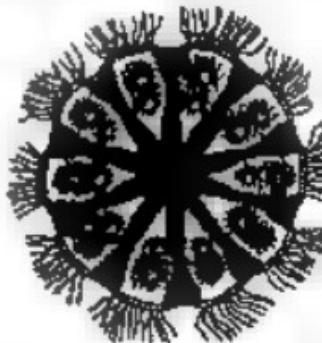
law, that their ancestors also were phylogenetically developed from a similar stem-cell. This ancient stem-form is the gastrula.

The gastrula probably lived in the sea during the Lower-Cambrian period, swimming about in the water by means of its ciliary coat, much as free-ciliated gastrulae do to-day. Probably it differed from the existing gastrulae only in one essential point, though extinct millions of years ago. We have reason, from comparative anatomy and embryology, to believe that it multiplied by sexual generation, not only asexually (by cleavage, germi-

**lution**.  
ation). We base these hypotheses on the fact that we do to-day find the simple forms of sexual reproduction among hydras and other lower animals, especially the coelenterates.

#### KINDS OF GASTRULA WITH AN ORGANIZING CELL OR HYPOTHECIA

There are not very many species of living gastrulae; but their morphological and phylogenetic interest is so great, an



... how the power of the division of the gastrula has been increased by a third process. Each cell has a new trophoblast as well as a nucleus.

their intermediate position between the Protozoa and Metazoa so instructive, that I proposed long ago (1876) to make a special class of them. I distinguished three orders in this class—the *Gastremaria*, *Phryniae*, and *Cynariae* (or *Dicyo-*

width). But we might also regard them as orders, as so many independent groups in a primitive gasterostean mass.

The Gasterosteidae and Cyclopoidea, the chief of them being gasterosteids, are small Meristina, that has gastrically branched after Metamere, and are, as a rule, 3 to 4 times as long, when much less (Fig. 23, 2-3). Their soft body, devoid of skeleton, consists of ten simple layers of cells, the primary gasterial layers; the edge of these is clearly defined with long cilia-like hairs, by which the posterior part gives almost to the various cavities of their body. The more gasterial layers form the greater products. The first layer of the original gaster (or *metapleura*) (Fig. 23, 1) is seen in the *Prostomatoidea gasterostea*, which Monnard discovered in the ovaries of a large modern *Pisces* (Anguilla) in 1889. The outer surface of the gaster was whitish, but covered with numerous of pale reddish, of 12 to 15 cells in diameter, in the fluid contents of which the little pores were very conspicuous. The expanded body of the *Prostomatoidea* (Fig. 23, 1) is somewhat reddish red, and showed that a red or orange or other deep colored ground has a vermicular. The simple layers of the cap (the posterior part of Fig. 23) have narrow openings (c.) The thin layer (c.) consists of long slender cylindrical cells, which have long ciliary hairs, it is separated by a thin structureless granulated plate (f.) from the ventral or gut layer (d.), the primitivo cells of which are much smaller and have no cilia. *Prostomatoidea* propagates sexually, by simple longitudinal cleavage; and this caused it to recently been regarded as the representatives of a special order of *Gasteropoda* (*Monopeltidae*).

Probably a near relative of the *Prostomatoidea* is the *Kamptozoa* (Ostracoda) (Fig. 23, a). It lives in the body cavity of *Vermes* (Sipunculans), and differs from the former in having no hollow older in the large whitish cells (c.) or the small tubercles (f.); the gasterial layers are separated by a thick, expanded, granular mass, which has been called the "clay-mud" (f.). The gastrulation is represented by a dark ring that bears very strong and long ciliary hairs, and affects the surrounding movements.

*Acanthocephala* and *Kamptozoa* may be included in the family of the *Gasteropoda*. As these gonostomes with eyes are not closely related the Ostracoda (Fig. 23, b, Fig. 23, 2-3). They long generally

including cavity of metapleura (Ostracoda) and vermicula; they are distinguished by the fact that their primitive gastrula is not empty, but filled with osmoticetic salts, from which the animal cells are developed. These gonostomes are of high class, the male (Fig. 23) being smaller and of a somewhat different shape from the oval female (Fig. 4).

The somewhat similar *Diplopoda* (Fig. 24) are distinguished from the preceding by the fact that their primitive gastrula is occupied by a single large ovaletum and composed of a crowded group of small cells. This cell does not yield small products, the afterwards division has a disorder of cells (several each of which, without being incorporated, grows into a small embryo). The *Diplopoda* live primarily in the body cavity especially the oral capsule of the exodermis. They live in worms, genera, some of which are distinguished by the presence of special setiferous pads. The body is numerous coiled, oval, or nephridial, or more often long and cylindric. The genus *Ceropales* (Fig. 24) differs from the ordinary *Diplopoda* in having their pair gonopods in the form of a sac, which may be enlarged terminally.

The classification of the *Copepoda* is much disputed, sometimes they are held to be primitive Infusoria (like the *Ostracoda*), sometimes planarians or annelids, related to the arachnid orders or rotifers, but having degenerated through parasitism, I adhere to the phylogenetic, morphological theory that I advanced in 1875. That we can find real gasterial products very rarely of the numerous other group of all the Meristina. In the struggle for life they have found shelter in the body cavity of other animals.

The small Copepoda included in the genus of the one that I have called the *Phrygionidae* (Heteropoda and *Ceropagidae*) probably form a third order for class of the living gasterostea. The genus *Phrygionidae* (Figs. 24, 1-2) is externally very similar to a large rhombus (surrounded by the more numerous sides) of the family of the *Acanthocephala*, which was at first taken for a sponge. In order to avoid confusion with them I afterwards gave them the name of *Phrygionidae*. The whole nervous body of the *Phrygionidae* is a simple cylindrical or oval tube with a transversal wall. The hollow of the tube is the ganglion cavity, and the upper opening of it is the mouth (Fig. 24, 2).

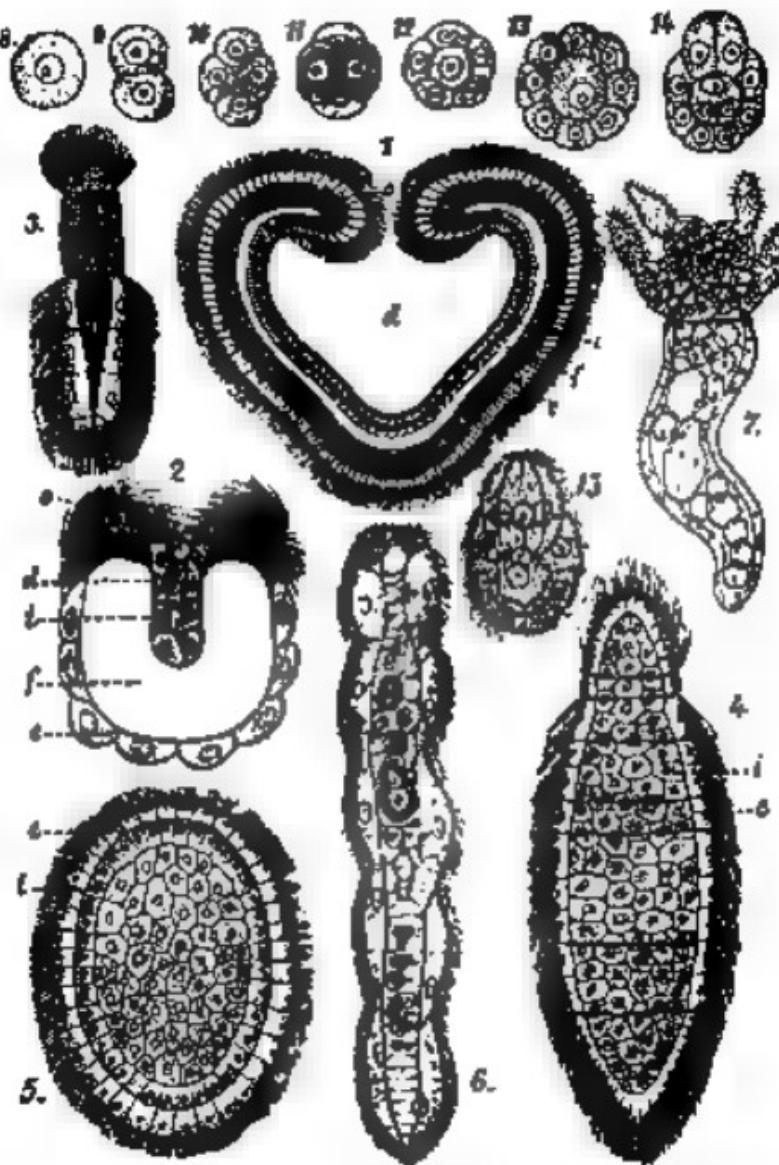


FIG. 216.—Modern protozoa. FIG. 1. *Paramecium perforatum*, C. M. Whipple, in longitudinal section. FIG. 2. *Stylonychia* (amoeboid). FIG. 3. *Amoeba* (amoeboid). FIG. 4. *Leucostichus* (amoeboid). FIG. 5. *Leucostichus* (amoeboid). FIG. 6. *Leucostichus* (amoeboid). FIG. 7. *Leucostichus* (amoeboid). FIG. 8. *Diaphrys* (radiolarian). FIG. 9. *Paramecium* (ciliate). FIG. 10. *Paramecium* (ciliate). FIG. 11. *Paramecium* (ciliate). FIG. 12. *Paramecium* (ciliate). FIG. 13. *Paramecium* (ciliate). FIG. 14. *Paramecium* (ciliate).

The two strata of cells that form the wall of the tube are the primary germinal layers. These rudimentary zooids differ from the ordinary zooids chiefly in being smaller and (as far as up to the floe)

In *Prophylloma* the primitive gut is a simple oral cavity, but in the closely related *Gastrophylloma* it is divided into two chambers by a transverse constriction, the broad and smaller chamber above furnishes the sexual products, the anterior one being for digestion.

The simplest sponges (*Olysma*, Fig. 231) have the same organization as the *Physellaria*. The only material difference between them is that in a sponge the thin two-layered body-wall is pierced by numerous pores. When these are closed they resemble the *Physellaria*. Possibly the gastrulae that we call *Physellaria* are only sponges with the pores closed. The *Ammothecium*, or the simple tubular sand-sponges of the deep seas (*Ammothecium*, etc.), do not differ from

— any weight until point when

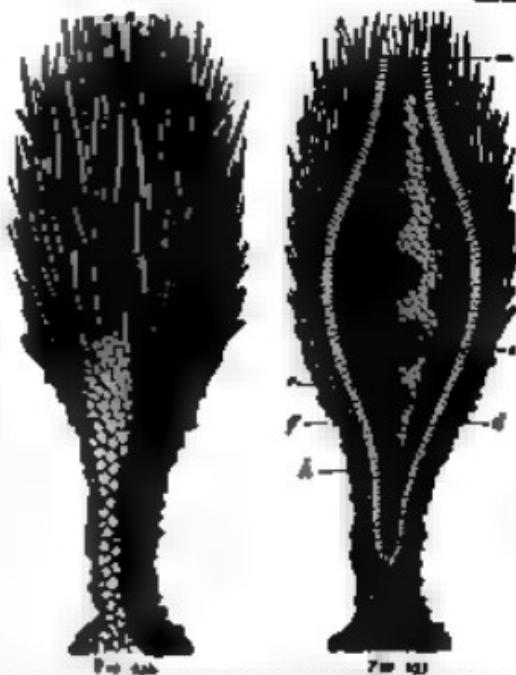


FIG. 230  
FIG. 231  
Two species of *Prophylloma*: *prophylloma*, a living specimen; *Fig. 230*. The shaft of the undivided animal (posterior side to the base of the oral). *Fig. 231*. The same in longitudinal section. The primitive gut (digestive canal) is the peristome, which becomes the digesting cavity (gastrocyst) in the marginal area (the "floe"). (After Schuchert.)



the pores are closed. In my Monograph on the Sponges (with sixty plates) I endeavored to prove analytically that all the species of this class can be traced phylogenetically to a common stem-form ("Calyptotheca").

The lowest form of the Cnidaria is also not far removed from the gastrulae. In the interesting common fresh-water polyp (*Hydra*) the whole body is simply an oval tube with a double wall; only in this case the mouth has a crown of tentacles. Before these develop the hydra requires an aecula (Figs. 236, 237). Afterwards there are slight histological differentiations in its ectoderm, through the ectoderm remains

——ectoderm of gastraphaea,  
in different stages. *Fig. 236*—ectoderm  
——ectoderm ——ectoderm

a single stratum of cells. We find the first differentiation of epithelial and



The epiblast, a very rudimentary organ. A cross is shown at the bottom.

stomachic cells, or of muscular and nervous cells, in the thick ectoderm of the hydros.

In all these rudimentary living coelenterates the sexual cells of both kinds—ova and sperms cells—are formed by the same individual; it is possible that the oldest metazoans were hermaphroditic. It is clear from comparative anatomy that hermaphroditism—the combination of both kinds of sexual cells in one individual—is the earliest form of sexual differentiation; the separation of the sexes (gonocidism) was a much later phenomenon. The sexual cells originally proceeded from the edge of the primitive mouth of the coelenterate.

## CHAPTER XX.

### OUR WORM-LIKE ANCESTORS

The gastrula theory has now convinced us that all the Metazoa or multicellular animals can be traced to a common stem-form, the Gastraea. In accordance with the biogeographic law, we find some proof of this in the fact that the two-layered embryos of all the Metazoa can be reduced to a primitive common type, the gastrula. Just as the countless species of the Mollusca do actually develop in the individual from the simple embryonic form of the gastrula, so they have all descended in part time from the common stem-form of the Gastraea. In this fact, and the fact we have already established that the Gastraea has been evolved from the hollow vesicle of the one-layered Blasma, and this again from the original unicellular stem-form, we have obtained a solid basis for our study of evolution. The close path from the stem-cell to the gastrula represents the first section of our human stem-history (Chapters VII., IX., and XIX.).

The second section, that leads from the Gastraea to the Prochordaria, is much more difficult and obscure. By the Prochordaria we mean the ancient and long-extinct animals which the important

embryonic form of the chordata proves to have been related (cf. Figs. 53-56). The nearest of living animals to this embryonic structure are the lowest Tunicates, the Copepoda (*Apylonautes*) and the larva of the Ascidia. As both the Tunicates and the Vertebrates develop from the same chordula, we may infer that there was a corresponding common ancestor of both stems. We may call this the Chordon, and the corresponding stem-group the Prochordians or Prochordata.

From this important stem-group of the unsegmented Prochordians (or "primitive chordal-animals") the stems of the Tunicates and Vertebrates have been divergently evolved. We shall see presently how this conclusion is justified in the present condition of morphological science.

We have first to answer the difficult and much discussed question of the development of the Chordata from the Gastraea; in other words, "How and by what transformations were the characteristic animals, resembling the embryonic chordula, which we regard as the common stem-forms of all the Chordata, both

Vertebrates and Vertebrates, evolved from the simplest two-layered Mammal?"

The descent of the Vertebrates from the Arthropoda has been maintained by a number of students during the last thirty years with more and than disagreement; and, as a result, no book has been written on the subject, we must deal with it in some detail. All these classes of Arthropoda in succession have been advanced the theory of being converted the "seed appendages" of the Vertebrates; first, the Annelida (Burkhardt, Lohman, and the like); then the Crustacea (Jensen, etc.); and, finally, the Trilobites (Spicer, Jensen, etc.). The most popular of these hypotheses was the annual theory, which derived the Vertebrates from the Worms. It was advanced simultaneously (1873) by Spiegel, of Wurzburg, and Anton Dehne, of Kiel. The latter developed this theory originally in favor of the falling degeneracy theory, with which I dealt in my work, *Anals and Methods of Animal Anthrology*.

This interesting degeneracy theory—pathetic discredited at that time, but almost forgotten now—was formed in 1873 with the aim of harmonizing the results of evolution and corresponding Darwinism with religious belief. The spiritual struggle that Dehne had experienced by the reiteration of the theory of descent in 1873, and that lasted for a decade with Marburg professors in every branch of Biology, was drawing to a close in 1875, and came out in the complete theory of transformation. To most of the degenerates the chief point was not the general question of evolution, but the particular one of "man's place in nature"—"The question of questions," as Huxley rightly called it. It was more evident to every semi-humane thinker that this question could only be answered in the state of man anthropogeny, by informing that man had descended from a long series of Vertebrates by gradual modification and improvement.

In this way the real affinity of man and the Vertebrates came to be admitted on all hands. Comparative anatomy and phylogeny alike was clearly for their heresy to be ignored no longer. But in order still to save man's unique position, and especially the degree of personal immortality, a number of natural philosophers and theologians discovered an admissible way of escape in the "theory of degeneration." Grounding the theory,

they turned the whole evolutionary theory upside down, and boldly contended that "man is not the most highly developed animal, but the insects are degenerate men." It is true that man is closely related to the ape, and belongs to the vertebrate class; but the state of his morality was supposed instead of denied. In the beginning "God created man in his own image," as the prototype of the perfect vertebrates; but, in consequence of original sin, the human race sank so low that the apes branched off from it, and afterwards the lower Vertebrates. When this theory of degeneration was sufficiently developed, no professor was bold to hold that the entire animal kingdom was descended from the degraded children of man.

This theory was most strenuously defended by the Catholic priest and natural philosopher, Michaelis, in his *Anthrologie*.<sup>1</sup> As Dehne's friend agreed Michaelis' Anthropology (1873). It will more "academic" and somewhat remote from the theory was advanced by a natural philosopher of the older Jena school—the mechanist and physiologist, Carl Snell. But it received its chief support to the metaphysical side from Anton Dehne, who modified the anthropomorphic ideas of Snell with particular ability. The Anthropos, which modern critics are about unanimously regards as the real Primitive Vertebrate, the modern model of the original vertebrate structure, is, according to Dehne, a low, degenerate descendant of the man, the "predator man" of the vertebrate family. It has descended from the Cyclostomes by a prolonged degeneration, and does in turn from the fishes; even the Annelids and the whole of the Trilobites are merely degenerate fishes! Following out this curious theory, Dehne says in contrast the genera, that the Cyclostomes and Worms are "lower animals"; he also claims that the unicellular Protists were degenerate Cyclostomes. In his opinion, "degeneration is the great principle that explains the existence of all the higher forms."

If this Michaelis-Dehne theory were true, and all animals were really degenerate descendants of an originally perfect humanity, one would naturally be the true centre and goal of all biological life; his anthropomorphic position and his immortality would be proved. Unfortunately, this created theory is in such

beginning contribution to all the known lines of paleontology and embryology that it is no longer worth serious scientific consideration.

But the case is no better for the much-discounted theory of the Vertebrates from the Annelids, which Debevoise afterwards maintained with gusto and. Of late years this hypothesis, which used to start dust and controversy, has been entirely abandoned by most competent zoologists, even those who once supported it. In chief support, Debevoise adduced in 1890 that it is "dead and buried," and made a hasty retraction at the end of his *Studies of the Early History of the Vertebrates*.

Now that the annelid-hypothesis is "dead and buried," and other attempts to derive the Vertebrates from Molluscs, Ctenophores, or Nematodes, have been equally unsuccessful, there is only one hypothesis left to answer the question of the origin of the Vertebrates—the hypothesis that I advanced thirty-five years ago and called the "annelid-hypothesis." In view of its sound foundation and its profound significance, it may very well claim to be a theory, and so should be described as the chordian or chordia theory.

I first advanced this theory in a series of university lectures in 1879, from which the *History of Creation* was composed. In the first edition of that work (1881) I endeavored to prove, on the strength of Kowalevsky's outstanding dissertation, that "of all the vertebrates known to us the Teleostei are undoubtedly the nearest blood-relatives of the Vertebrates; they are the most closely related to the Vertebrates, from which the Vertebrates have been derived. Naturally, I do not state that the Vertebrates have descended from the Teleostei, but that the two groups have sprung from a common stock. It is clear that the real Vertebrates (primarily the Acanthocephala) were evolved in very early times from a group of Worms, from which the degenerate Teleostei also descended in smaller and retrogressive directions." This curious extract now-group art the Pachystomidae; we will have a reference of ours in the chordian-theory of the Vertebrates and Teleostei; and they will exist independently, in very modified form, in the class of the Cyclopidae (Gegenbaur, Fig. 292).

The chordian-theory received the most weighty and complete support from

Carl Gegenbaur. This able comparative zoologist defended it in 1876, in the second edition of his *Elements of Comparative Anatomy*; at the same time he drew attention to the important relations of the Teleostei to a various group, the Chondrosteans. He rightly regards this as the representative of a special class of worms, which he called "spine-branched" (*Chordoporellae*). Gegenbaur referred in many other papers to the close blood-relationship of the Teleostei and Vertebrates, and lucidly explained the reasons that justify us in framing the hypothesis of the descent of the two groups from a common ancestor, an unsegmented vertebrate, situated in the axial chord between the dorsal peritoneum and the ventral gut-tube.

The theory afterwards received a good deal of support from the researches made by a number of distinguished zoologists and paleontologists, especially L. Huxley, B. Macfie, F. Balfour, G. Van Beneden, and Jules. Since Macfie's *Nature of the Development of the Amphioxus* gives us full information as to the embryology of this famous vertebrate, it has become so important for our purpose that we must consider it a document of the first rank for answering the question we are dealing with.

The embryonic facts that we gather from this old survivor of the Acorn worms are the more valuable for phylogenetic purposes, as paleontology, under kindly favor, has fought a hard battle on the origin of the Vertebrates. These invertebrate ancestors were soft organisms without skeleton, and less capable of fossilization, so to odd the ones with the least vertebrates—the Acorn worms and Cyclostomes. The ones closest to the greater part of the Vertebrates or vertebrate ancestors, the various classes and orders of which differ so much in structure. The isolated groups of the rush stem are living branches of a large tree, the greater part of which has long been dead, and we have no fossil evidence as to its earlier form. Nevertheless, some of the neighboring groups are very instructive, and give us clear indications of the way in which the Chordata were developed from the Vermes, and then from the Cyclostomes.

While we seek the most important of these embryonic forms among the groups of Cyclostomes and Vertebrates, it is evident that not a single one of them

must be regarded as an unchanged, or even little changed, copy of the ancient larval form. One group has remained one feature, another a different feature of the original organization, and other organs have been further developed and characteristically modified. Hence from, more than in any other part of our genealogical tree, we have to keep before our minds the full picture of development, and separate the successive secondary phenomena, from the ancestral and primary. It will be useful first to pick out the chief advances in organization by which the simple Cnidaria gradually became the more developed Ctenophores.

We find our best and safest basis in the journals of the Amphioxon (Fig. 39) the bilaterally and triradiately symmetrical larva of all the Metazoa—selected at an early stage into two divergent groups. The ancestral Cnidaria became sessile, and gave rise to two forms, the Siphonophores and the Ctenophores (the latter all radially symmetrical polyzoa like the hydra). But the first Ctenophores adopted a certain type of division of the body as a result of the predominance of ciliary movement, and it is easier to assume that it was a great advantage to insure the border equally between the two halves of the body (right and left). Thus came the radial bilateral form, which has three arms. The more bilateral type is found in all the advanced forms of Anthozoa—corals, etc., &c., & it is to be the basis for the development of the body in a certain direction and steady progress. Bilateral radial division easily developed the bilateral type in a number of the Ctenophores and then produced the meta-forms of all the bilateral animals.

The Ctenophores, of which we may consider the bilateral genera of the Anthozoa as by a palaeogenetic representation, represented the two-valved organisms of the earliest Metazoa in its simplest form. The vegetal endoderm that had then already greatly served for nutrition; the ciliated protostom that turned the external skin ectoderm to locomotion and nutrition; finally the two primitive metacercaridial ova, that lay to the right and left in the ventral border of the primitive gonopore, were sexual ova, and effected reproduction. In order to understand the further development of the genera, we must pay particular attention to: (1) the general study of the metapolytic stages of the embryo; that the larvae are

graptozoa and the rhizoids; (2) the morphological study of the simplest Thaliidae (*Phorbas* and *Turritellula*) and various groups of anarchozoan Vermiformia (*Lamellibranchia*, *Micromesistia*, *Entoproctida*).

We have to consider the Placodes first, because they are on the border between the two principal groups of the Metazoa, the Ctenophores and the Cnidaria. While the former they show the lack of individual, nerve, and vascular system; while the latter they have in common the bilateral type, the possession of a pair of nephridia or renal canals, and the formation of a central brain or cerebral ganglion. It is now used to distinguish four classes of Placodes: the two free-living forms of the primitive worms (*Platynereis*), and the aged worms (*Festucalex*), and the two peculiar classes of the metazoan worms (*Threptomyia* and the tape-worms (*Cestoda*)). We have only to consider the first two of these classes. The other two are parasitic, and have descended from the former by adaptation to parasitic habits and consequent degeneration.

The primitive worms (*Platynereis*) are very much like worms of simple construction, but of great morphological and physiological interest. They have been hitherto at a rate regarded as a special order of the Turritellidae, and associated with the Anthozoa, but they differ considerably from them and all the other Placodes that entered in the absence of renal canals and a special central nervous system, the structure of their skins at the simpler class of the older Placodes. Most of the Placodes of the group (*Aplochitonidae*, *Aplidioteridae*, *Chloriidae*, *Ascidioidea*, etc.) are very soft and delicate animals, swimming about in the sea by means of a ciliary veil, and very small (up to 4 mm long). Their oral body, without appendages, is sometimes pyriform-shaped or cylindroid, sometimes flat and broad-shaped. Their skin is merely a layer of ciliated epidermic cells. Under this is a soft medullary substance, which consists of rounded cells with nucleus. The food passes through the mouth directly into this singular middle layer substance, in which we do not generally see any permanent gut-walls (it may have recently collapsed); hence these primitive Placodes have been called Asciids (without gut-walls or *coeloma*), or, equivalently, Cystozoans, or *Placozoa*. The main organ of these Ctenophores

Platids are very simple—two pairs of strings of cells, the bases of which (the ovaries, Fig. 234 a) produce eggs, and the bases (the spermatids, b) sperm-cells. These glands are not yet differentiated, sexual glands, but merely differentiated cell-groups in the undifferentiated substance, or, in other words, parts of the germinal. Their products, the eggs and sperm, are covered over behind by two pairs of short muscle;

that lies underneath is rather thick, and represents the first rudiment of a neural ganglion (vertical brain or aereopaglion).

The *Fusculiferia*, with which the simpler Platids were formerly classed, differ essentially from them in the more advanced structure of their organs, and especially in having a central nervous system (vertical brain and sensory road cords (neuroptiles); both originate from the antennae. But between the two germinal layers a mesoderm is developed, a sort of connective tissue, in which the organs are embedded. The *Turbellaria* are still represented by a number of different forms, in both fresh and sea-water. The oldest of them are the very rudimentary and they show that are known as *Strobiloids* as precursors of the simple construction of their gut; they are, as a rule, less than a quarter of an inch long, and of a simple oval or lanceolate shape (Fig. 242). The surface is covered with ciliated epithelium, a stratum of ciliated cells. The digestive gut is still the simple primitive gut of the gastrula (d), with a single aperture that is both mouth and anus (e). There is, however, an invagination of the ectoderm at the mouth, which has given rise to a muscular pharynx (f). It is noteworthy that the mouth of the *Turbellaria* (like the primitive mouth of the Coelenterates) lies, in the class, change its position considerably in the middle part of the ventral surface; sometimes it is situated (in *Clavelinæ*), sometimes in the middle (in *Monogeneans*), sometimes in front (in *Platodes*). This displacement of the mouth from front to rear is very interesting, because it corresponds to a phylogenetic displacement of the mouth.

This probably occurred in the Platodes sections of molls (or all of the Cephalopoda); in these the primitive mouth (metapleural) lies at the fore end (oral) pole, whereas the primitive mouth (prostomial) lies at the hind end of the bilaterally body. In most of the *Turbellaria* there is a narrow cavity, containing a number of secondary organs, between the two primary germinal layers, the outer or external layer of which forms the epidermis and the inner, vegetal layer the visceral epithelium. The earliest of these organs are the excretory organs; they are very variously constructed in the Platodes class; in the simplest case there are scarcely two pairs of glands or sexual glands—a pair of testes (Fig. 243)

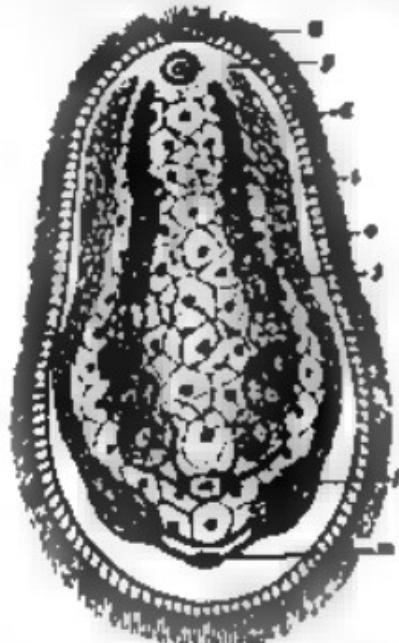


FIG. 242.—*Strobiloides* (Leng & Müller). A transverse section of the viviparous larva of the genus *Strobiloides* or *Strobila*. The two pairs of the primary germinal layers are seen at the bottom above the gut. The gut is shown in longitudinal section, and the oviduct and spermatid ducts are seen in relation to it. The nervous system is shown passing through the epidermis.

or rectal opening (e) lies just behind the female (f). Most of the *Turbellaria* have lost the muscular pharynx, which is very advanced in the *Turbellaria* and *Platids*. On the other hand, they have, as a rule, bodies or behind the mouth, a bilobed non-ciliated (empty) vesicle or organ of equilibrium, g; and many of them have also a simple or simple optic spots. The ciliates of the ectoderm

in most of the *Turbellaria* there is a narrow cavity, containing a number of secondary organs, between the two primary germinal layers, the outer or external layer of which forms the epidermis and the inner, vegetal layer the visceral epithelium. The earliest of these organs are the excretory organs; they are very variously constructed in the Platodes class; in the simplest case there are scarcely two pairs of glands or sexual glands—a pair of testes (Fig. 243)

and a pair of ovaries (*o.*). They open externally, sometimes by a common aperture (*Mesogonophores*), sometimes by separate ones, the female behind the male (*Digonophores*, Fig. 241). The sexual glands develop originally from the two proctonephridia or primitive metanephridial cells (Fig. 83 *a*). As these earliest metanephridial structures extended, and became vacuous sexual pouches in the later descendants of the Platydes, probably the two coelom-pouches were formed from them, the first trace of the real body-cavity of the higher Metazoa (*Metacercariae*).

The gonads are among the oldest organs, the few other organs that we find in the Platydes between the gut-wall and body-wall being later evolutionary products. One of the oldest and most important of these are the kidneys or nephridia, which remove unusable matter from the body (Fig. 240 *not*). These urinary or excretory organs were originally enlarged skin-glands—a couple of oesacs that run the length of the body, and have a separate or common external aperture (*not*). They often have a number of branches. These special excretory organs are not found in the other *Moneraria* (Ostreopods, Sponges, Ciliates) or the *Cryptozoa*. They are first met in the *Turbellaria*, and have been transmitted almost from these to the *annelids*, and from those to the higher stars.

Finally, there is a very important new organ in the *Turbellaria*, which we do not find in the *Cryptozoa* (Fig. 239) and their gastrulae ancestors—the radicular nervous system. It consists of a couple of simple cerebral ganglia (Fig. 141 *g*) and fine nervous fibers that radiate from them; these are partly voluntary nerves (or motor fibers) that go to the thin muscular layer developing under the skin; and partly sensory nerves that proceed to the sense-cells of the ciliated epidermis (*ff.*). Many of the *Turbellaria* have also special sense-organs; a couple of ciliated smell pits (*os.*), rudimentary eyes (*es.*), and, less frequently, auditory vesicles.

On these principles I assume that the oldest and simplest *Turbellaria* arose from *Platydesmus*, and these directly from bilateral *Gastrulae*. The chief advances were the formation of gonads and nephridia, and of the radicular nervous. On this hypothesis, which I advanced in 1879

in the first sketch of the *Gastraea-theory* (*Monograph on the Spiralia*), there is no direct affinity between the *Platydes* and the *Ciliates*.

Next to the ancient stem-group of the *Turbellaria* comes a number of more recent chordous ancestors, which we class with the *Nemertea* or *Heterotela*, the unsegmented worms. These true



FIG. 240.—A longitudinal section of *Turbellaria*, showing the gut, midgut, proctonephridia, kidneys, nerve-cells, nerve-fibres, cilia, epidermis, muscular-layer, body-wall, and gills. (Diagram.)

FIG. 241.—The same, showing the gut, midgut, ovaries, proctonephridia, kidneys, nerve-cells, nerve-fibres, cilia, epidermis, muscular-layer, body-wall, and gills. (Diagram.)

worms (Nemertea, lately also called *Jelly-cells*) are the difficulty of the higher-term of the zoological classifier, because the various classes have very complicated relations to the lower *Platydes* on the one hand and the more advanced animals on the other. But if we exclude the *Platydes* and the *Annelids* from this stem, we find a fairly satisfactory unity of organization

in the remaining classes. Among these worms we find some important forms that show considerable advance in organization from the platodes to the chaetognath stage. Three of these phenomena are particularly instructive: (1) The formation of a true (secondary) body-cavity (coeloma); (2) the formation of a second aperture of the gut, the anus; and (3) the formation of a vascular system. The great majority of the Vermalia have these

of us eyes at the posterior end (Fig. 242 a). Further, the cilia that cover the whole surface of the Turbellaria are confined in the Gastrotricha to two ciliary bands (f) on the ventral surface of the oral body, the dorsal surface having friction. Otherwise the organization of the two classes is the same. In both the gut consists of a muscular gullet (e) and a slender pedisitic gut (d). Over the gullet is a double brain (cereganglion, g)

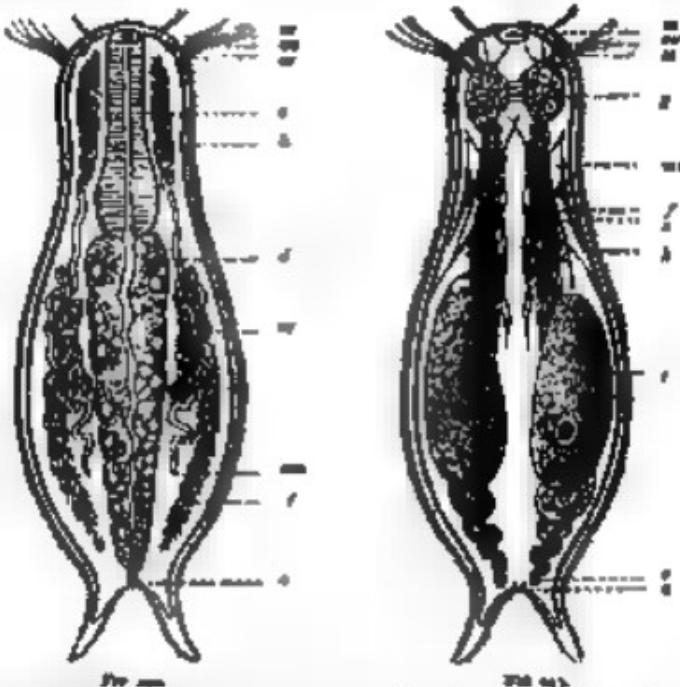


FIG. 242 a & b.—Gastrotrichs. A transverse section of the group of Ostracorhynchus, or mouth-gulper, a form  $\frac{1}{2}$  mm. long, a nervous system with a large anterior ganglion, & two ciliary bands of the ventral surface as depicted, and their sections, a, b.

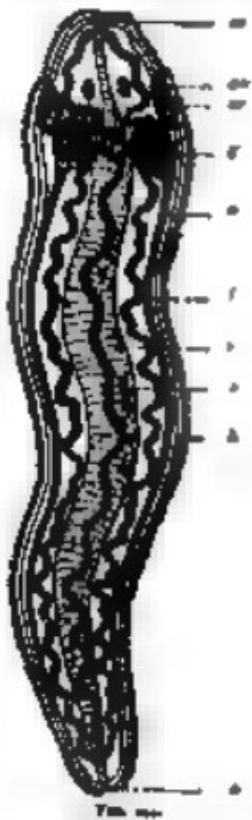
three features, and they are all wanting in the Platodes; in the rest of the worms at least one or two of them are developed.

Next and very close to the Platodes we have the Ichthydina (Gastrotrichs), little marine and fresh-water worms, about  $\frac{1}{16}$  to  $\frac{1}{8}$  inch long. Zoolologists differ as to their position in classification. In my opinion, they approach very closely to the Rhabdocephala (Figs. 243, 244), and differ from these chiefly in the presence

at the side of the gut are two sorptional pressure canals (water-vessels or periaqueductal, m), which open on the ventral side (mm.). Behind are a pair of simple sexual glands or gonads (Fig. 243 r).

While the Ichthydina are thus closely related to the Platodes, we have to go further away for the two classes of Vermalia which we unite in the group of the "mud-worms" / Frontalia/. These are the Nematoda and the Enteropneusta

Both classes have a complete circulatory system on the epidermis, a heritage from the Turbellaria and the Gastropoda; also, both have two openings of the gut, the mouth and anus, like the Gastrotricha. But we find also an important organ that is wanting in the preceding forms—the vascular system. In their more advanced annelids we find a few coenocytic longitudinal canals which force the blood through the body by their contractions; these are the first blood-vessels.



The app.—A simple Description. to consist of one or more, & larger, & more or less hairy Glands, for holding & grasping (the seeds), an eye, & several tentacles, & appendages. (Diagram.)



The Nemertines were formerly classed with the much less advanced Turbellaria, but they differ essentially from them in having an anus and blood-vessels, and several other marks of higher organization. They have generally long and narrow bodies, like a wire or hair flattened, and; there are, besides several small species, giant-forms with a width of 5 to 8 inches and a length of several yards (even up to fifteen). Most of them live in the sea, but some in fresh water and marine marsh. In their internal structure they approach the Turbellaria on the one hand and the higher Vermiformia (especially the Enteropneusts) on the other. They have a good deal of interest as the lowest and oldest of all animals with blood. In them we find blood-vessels for the first time, distributing real blood through the body.



Fig. 244.—Arrangement of the tracheal gas vesicle. A, circular cross-section of a Nemertine; B, longitudinal section, showing how it lies between the gut and the epidermis, and how it opens into the epidermal or hypodermic groove (v) at the anterior and hypodermic groove (d) at the posterior end.

The blood is red, and the red colouring-matter is haemoglobin, associated with elliptic discoid blood-cells, as in the Vermiformia. Most of them have two or three parallel blood-canals, which run the whole length of the body, and are connected in front and behind by loops, and often by a number of ring-shaped pieces. The third of these primitive blood-vessels is the one that lies above the gut in the middle line of the back (Fig. 244 *v*). It may be compared to either the dorsal vessel of the Articulata or the notis of the Vermiformia. To the right and left are the two vertebral lateral vessels (Fig. 244 *B*).

After the Nemertines, I take (as distinct relatives) the Enteropneusts: they may be classed together with them as *Amphioxus* or *Aphyosoma* (moss-worms). There is now only one genus of this class, with several species (*Dendrodoa*); but it

is very remarkable, and may be regarded as the last survivor of an ancient and long-extinct class of Vertebrates. They are related, on the one hand, to the Nematodes and their immediate ancestors, the Platydes, and to the lowest and oldest fauna of the Chondriota on the other.

The Enteropneusts (Fig. 245) live in the sea sand, and are long worms of very simple shape, like the Nemertines. From the latter they have inherited: (1) The bilaterally symmetrical segmentation; (2) the ciliary coat of the soft epidermis; (3) the double rows of gastric pouches, alternating with a single or double row of glands; (4) separation of the gut (the Platides ancestors were hercophylic); (5) the ventral mouth, supplementing a protruding esophagus; (6) the gut terminating in the rectal glandulae; and (7) ventral parallel blood-vessels, running the length of the body, a dorsal and a central principal stem.

On the other hand, the Enteropneusts differ from their Nemertine ancestors in several features, some of which are important, others of which are attributable to adaptation. The chief of these is the branchial gut (Fig. 245 *A*). The anterior portion of the gut is converted into a respiratory organ, and placed by the side of gill-slits: between these there is a branched (grill) epithelium, formed of rods and plates of collagen. The water that enters

at the mouth makes its exit by these slits. They lie in the dorsal half of the fore-gut, and this is completely separated from the ventral half by two longitudinal folds (Fig. 245 *A'*). This ventral half, the gill-foliate walls of which are clothed with ciliary epithelium and secrete mucus, corresponds to the pharyngeal or hypobranchial groove of the Chondriota (Fig. 246), the respiratory organ from which the later lobped gland is developed in the Craniota (cf. p. 184). The agreement in the structure of the branchial gut of the Enteropneusts, Turbellaries, and Vertebrates was first recognised by Gegenbaur (1872); it is the more significant as at first we find only a couple of gill-slits in the young animals of all three groups; the number gradually increases. We can infer from this the common descent of the three groups with all the more

confidence when we find the *Balanoglossus* approaching the Chordons in other respects. Thus, for instance, the chief part of the central nervous system is a long dorsal neural string that runs above the gut and corresponds to the medullary tube of the Chordons. Bateson believes he has detected a rudimentary chorda between the two.

Of all extant invertebrate animals the Enteropneusts come nearest to the Chordons in virtue of these peculiar characters, hence we may regard them as the survivors of the ancient gut-bearing Vermalia from which the Chordons also have descended. Again, of all the chord-animals, the Copeiata (Fig. 225) and the larval forms of the ascidians approach nearest to the young *Balanoglossus*. Both are, on the other hand, very closely related to the Ascidians, the Primitive Vertebrates of which we have considered the importance (Chapters XVI. and XVII.). As we saw there, the unsegmented Tunicates and the articulated Vertebrates must be regarded as two independent stems, that have developed in divergent directions. But the common root of the two stems, the ascidian group of the Prochordons, must be sought in the vermalian stem; and of all the living Vermalia those we have considered give us the safest clue to their origin. It is true that the several representatives of the important groups of the Copeiata, Balanoglossid, Nematodes, Ichthyidae, etc., have more or less departed from the primitive model owing to adaptation to special environment. But we may just as confidently affirm that the main features of

their organization have been preserved by heredity.

We must grant, however, that in the whole annals history of the Vertebrates the long stretch from the Gastrulae and Planulas up to the oldest Chordons remains by far the most obscure section. We might frame another hypothesis to relieve this difficulty—namely, that there was a long series of very different and totally extinct forms between the Gastrulae and the Chordons. Even in this modified chorda-theory the six fundamental organs of the chorda would retain their great value. The medullary tube would be originally a chemical sensory organ, a dorsal olfactory tube, taking in respiratory-water and food by the neuroseptae in front and conveying them by the aeroenteric canal into the primitive gut. This olfactory tube would afterwards become the nervous centre, while the expanding gonads lying to right and left of the primitive mouth would form the coelome. The chorda may have been originally a digestive glandular groove in the dorsal middle line of the primitive gut. The two secondary gut-openings, mouth and anus, may have arisen in various ways by change of functions. In any case, we should ascribe the same high value to the chorda as we did before to the gastrula.

In order to explain more fully the chief stages in the advance of our race, I add the hypothesis sketch of man's ancestry that I published in my *Zoist* [a translation by Dr. Uddow of the paper read at the International Zoological Congress at Cambridge in 1898].—

A.—*Man's* Genealogical Tree, First Half:  
EARLIER SERIES OF ANCESTORS, WITHOUT  
POSSIL EVIDENCE.

B.—*Man's* Genealogical Tree, Second Half:  
LATER ANCESTORS, WITH FOSSIL EVIDENCE.

EARLY STAGES.	ANCESTRAL HUMAN	LATER STAGES OF HUMANITY
1. <i>Homo erectus</i>		
2. <i>Homo heidelbergensis</i>		
3. <i>Homo neanderthalensis</i>		
4. <i>Homo sapiens</i>		
5. <i>Chimpanzee</i>		
6. <i>Gorilla</i>		
7. <i>Pan troglodytes</i>		
8. <i>Pan paniscus</i>		
9. <i>Orangutan</i>		
10. <i>Gibbon</i>		
11. <i>Proboscidean</i>		
12. <i>Mammal</i>		
13. <i>Reptile</i>		
14. <i>Amphibian</i>		
15. <i>Insect</i>		
16. <i>Crustacean</i>		
17. <i>Fish</i>		
18. <i>Amphioxus</i>		
19. <i>Coelenterate</i>		
20. <i>annelid</i>		
21. <i>echinoderm</i>		
22. <i>mollusk</i>		
23. <i>fish</i>		
24. <i>arthropod</i>		
25. <i>annelid</i>		
26. <i>echinoderm</i>		
27. <i>mollusk</i>		
28. <i>fish</i>		
29. <i>arthropod</i>		
30. <i>annelid</i>		
31. <i>echinoderm</i>		
32. <i>mollusk</i>		
33. <i>fish</i>		
34. <i>arthropod</i>		
35. <i>annelid</i>		
36. <i>echinoderm</i>		
37. <i>mollusk</i>		
38. <i>fish</i>		
39. <i>arthropod</i>		
40. <i>annelid</i>		
41. <i>echinoderm</i>		
42. <i>mollusk</i>		
43. <i>fish</i>		
44. <i>arthropod</i>		
45. <i>annelid</i>		
46. <i>echinoderm</i>		
47. <i>mollusk</i>		
48. <i>fish</i>		
49. <i>arthropod</i>		
50. <i>annelid</i>		
51. <i>echinoderm</i>		
52. <i>mollusk</i>		
53. <i>fish</i>		
54. <i>arthropod</i>		
55. <i>annelid</i>		
56. <i>echinoderm</i>		
57. <i>mollusk</i>		
58. <i>fish</i>		
59. <i>arthropod</i>		
60. <i>annelid</i>		
61. <i>echinoderm</i>		
62. <i>mollusk</i>		
63. <i>fish</i>		
64. <i>arthropod</i>		
65. <i>annelid</i>		
66. <i>echinoderm</i>		
67. <i>mollusk</i>		
68. <i>fish</i>		
69. <i>arthropod</i>		
70. <i>annelid</i>		
71. <i>echinoderm</i>		
72. <i>mollusk</i>		
73. <i>fish</i>		
74. <i>arthropod</i>		
75. <i>annelid</i>		
76. <i>echinoderm</i>		
77. <i>mollusk</i>		
78. <i>fish</i>		
79. <i>arthropod</i>		
80. <i>annelid</i>		
81. <i>echinoderm</i>		
82. <i>mollusk</i>		
83. <i>fish</i>		
84. <i>arthropod</i>		
85. <i>annelid</i>		
86. <i>echinoderm</i>		
87. <i>mollusk</i>		
88. <i>fish</i>		
89. <i>arthropod</i>		
90. <i>annelid</i>		
91. <i>echinoderm</i>		
92. <i>mollusk</i>		
93. <i>fish</i>		
94. <i>arthropod</i>		
95. <i>annelid</i>		
96. <i>echinoderm</i>		
97. <i>mollusk</i>		
98. <i>fish</i>		
99. <i>arthropod</i>		
100. <i>annelid</i>		

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7. <i>Pan troglodytes</i>		
8. <i>Pan paniscus</i>		
9. <i>Orangutan</i>		
10. <i>Gibbon</i>		
11. <i>Proboscidean</i>		
12. <i>Mammal</i>		
13. <i>Reptile</i>		
14. <i>Amphibian</i>		
15. <i>Insect</i>		
16. <i>Crustacean</i>		
17. <i>Fish</i>		
18. <i>Amphioxus</i>		
19. <i>Coelenterate</i>		
20. <i>annelid</i>		
21. <i>echinoderm</i>		
22. <i>mollusk</i>		
23. <i>fish</i>		
24. <i>arthropod</i>		
25. <i>annelid</i>		
26. <i>echinoderm</i>		
27. <i>mollusk</i>		
28. <i>fish</i>		
29. <i>arthropod</i>		
30. <i>annelid</i>		
31. <i>echinoderm</i>		
32. <i>mollusk</i>		
33. <i>fish</i>		
34. <i>arthropod</i>		
35. <i>annelid</i>		
36. <i>echinoderm</i>		
37. <i>mollusk</i>		
38. <i>fish</i>		
39. <i>arthropod</i>		
40. <i>annelid</i>		
41. <i>echinoderm</i>		
42. <i>mollusk</i>		
43. <i>fish</i>		
44. <i>arthropod</i>		
45. <i>annelid</i>		
46. <i>echinoderm</i>		
47. <i>mollusk</i>		
48. <i>fish</i>		
49. <i>arthropod</i>		
50. <i>annelid</i>		
51. <i>echinoderm</i>		
52. <i>mollusk</i>		
53. <i>fish</i>		
54. <i>arthropod</i>		
55. <i>annelid</i>		
56. <i>echinoderm</i>		
57. <i>mollusk</i>		
58. <i>fish</i>		
59. <i>arthropod</i>		
60. <i>annelid</i>		
61. <i>echinoderm</i>		
62. <i>mollusk</i>		
63. <i>fish</i>		
64. <i>arthropod</i>		
65. <i>annelid</i>		
66. <i>echinoderm</i>		
67. <i>mollusk</i>		
68. <i>fish</i>		
69. <i>arthropod</i>		
70. <i>annelid</i>		
71. <i>echinoderm</i>		
72. <i>mollusk</i>		
73. <i>fish</i>		
74. <i>arthropod</i>		
75. <i>annelid</i>		
76. <i>echinoderm</i>		
77. <i>mollusk</i>		
78. <i>fish</i>		
79. <i>arthropod</i>		
80. <i>annelid</i>		
81. <i>echinoderm</i>		
82. <i>mollusk</i>		
83. <i>fish</i>		
84. <i>arthropod</i>		
85. <i>annelid</i>		
86. <i>echinoderm</i>		
87. <i>mollusk</i>		
88. <i>fish</i>		
89. <i>arthropod</i>		
90. <i>annelid</i>		
91. <i>echinoderm</i>		
92. <i>mollusk</i>		
93. <i>fish</i>		
94. <i>arthropod</i>		
95. <i>annelid</i>		
96. <i>echinoderm</i>		
97. <i>mollusk</i>		
98. <i>fish</i>		
99. <i>arthropod</i>		
100. <i>annelid</i>		

## CHAPTER XXI.

### OUR FISH-LIKE ANCESTORS

Our task of detecting the earliest ancestors of our race among the vast numbers of animals known to us encounters very different difficulties in the various sections of man's stem-history. These were very great in the series of our invertebrate ancestors; they are much slighter in the subsequent series of our vertebrate ancestors. Within the vertebrate stem there is, as we have already seen, so complete an agreement in structure and embryology that it is impossible to doubt their phylogenetic unity. In this case the evidence is much clearer and more abundant.

The characteristics that distinguish the Vertebrates as a whole from the Invertebrates have already been discussed in our description of the hypothetical Primitive Vertebrate (Chapter XI., Pigs. 98-102). The chief of these are: (1) the evolution of the primitive brain (i.e. a dorsal tubular tube), (2) the formation of the chorda between the mouth-tube and the gut, (3) the division of the gut into fore-, middle- (gut) and hind-gut (rectum) gas, and (4) the internal articulation or segmentation. The first three features are shared by the Vertebrates with the Ascidiacids and the Prochordians, the fourth is peculiar to them. That the chief advantage in organisation by which the earliest Vertebrates took precedence of the unsegmented Chordians consisted in the development of internal segmentation.

The whole vertebrate stem divides first into the two chief sections of Acrania and Craniota. The Amphioxus is the only surviving representative of the older and lower section, the Acrania ("shell-less"). All the other vertebrates belong to the second division, the Craniota ("skull-animals"). [The Craniota descend directly from the Acrania, and these from the primitive Chordians.] The comparative study that we made of the comparative anatomy and ontogeny of the Acrania and the Amphioxus has proved these relations for us. (See Chapters XVI. and XVII.)

The Amphioxus, the lowest Vertebrate, and the Acrania, the nearest related Invertebrate, descend from a common earliest stem-form, the Chordia; and this must have had, substantially, the organisation of the chordia.

However, the Amphioxus is important not merely because it fills the deep gulf between the Invertebrates and Vertebrates, but also because it shows us to-day the typical vertebrate in all its simplicity. We owe to it the most important data that we possess in reconstructing the greatest historical development of the whole race. All the Craniota descend from a common stem-form, and this was substantially identical in structure with the Amphioxus. This stem-form, the Primitive Vertebrate (*Primitivius*, *Fig. 98-102*), had the characteristics of the chordia as such, but not the important features that distinguish the Craniota from the Acrania. Though the Amphioxus has many peculiarities of structure and has much degenerated, and though it cannot be regarded as an unchanged descendant of the Primitive Vertebrate, it still has inherited from it the specific characters we enumerated above. We may not say that "Amphioxus is the ancestor of the Vertebrates"; but we can say: "Amphioxus is the nearest relation to the ancestor of all the animals we know." Both belong to the same small family, or lowest class of the Vertebrates, that we call the Acrania. In our genealogical tree this group forms the twelfth stage, or the first stage among the vertebrate ancestors (p. 102). From this group of Acrania both the Amphioxus and the Craniota were evolved.

The next division of the Craniota embraces all the Vertebrates known to us, with the exception of the Amphioxus. All of these have a head clearly differentiated from the trunk, and a skull enclosing a brain. The head has also three pairs of higher sense-organs (nose, eyes, and ear). The brain is very rudimentary at first, a mere hollow enlargement of the

flat-out of the mandibular teeth. But it is soon divided by a number of transverse constrictions into, first three, then five successive cerebral vesicles. In this formation of the head, skin, and brain, with further development of the higher vertebrates, we have the advance that the Craniota made beyond their shield-less ancestors. Other organs also attained a higher development; they acquired a compact central heart with valves and a more advanced liver and kidneys, and made progress in other important respects.

We may divide the Craniota generally into Cyclostoma ("round-mouthed") and Gnathostoma ("jaw-mouthed"). There are only a few groups of the former to estimate now, but they are very interesting, because in their whole structure they stand midway between the Actinaria and the Gnathostomata. They are much more advanced than the Actinaria, much less so than the fishes, and these form a very welcome connecting-link between the two groups. We may therefore consider them a special intermediate group, the fourteenth and fifteenth stages in the series of our ancestors.

The few surviving species of the Cyclostoma are divided into two orders—the Myxini and the Petromyzontida. The former, the long-

fishes, have a long, cylindrical, worm-like body. They were classed by Linnaeus with the worms, and by later zoologists with the fishes, or the amphibia, or the molluscs. They live in the sea, normally as parasites of fishes, into the skin of which they bore with their rasped suction mouth and their tentacles, armed with horny teeth. They are sometimes found alive in the body-cavity of fishes (such as the torp or sturgeon); in those cases they have passed through the skin into the interior. The second order consists of the Petromyzontida or lampreys; the small river lamprey (*Petromyzon fluminalis*) and the large marine lamprey (*Petromyzon marinus*, Fig. 227). They also have a round suction mouth, with horny teeth inside it; by means of this they attach themselves by sucking to fishes, stones, and other objects (hence the name *Atrypa* = stone-sucker). It seems that this habit was very widespread among the earlier Vertebrates; the larvae of many of the Cephalopods and frogs have muscular disks near the mouth.

The class that is formed of the Myxini and Petromyzontida is called the Cyclostoma (round-mouthed), because their mouth has a circular or semi-circular aperture. The jaws (upper and lower) that we find in all the higher Vertebrates are completely wanting in the Cyclostoma, as in the Amphibia. Hence the other Vertebrates are collectively opposed to them as Gnathostoma (jaw-mouthed). The Cyclostoma might also be called *Amphineuri* (single-nosed), because they have only a single nasal passage, while all the Gnathostomata have two nostrils (Agnathous = double-nosed). But apart from these peculiarities the Cyclostoma differ from vertebrates like the fishes in other special features of their structure than the fishes do from man. Hence they are obviously the last survivors of a very ancient class of Vertebrates, that was far from attaining the advanced organization of the true fish. To mention only the chief points, the Cyclostoma show no trace of trace of bone. Their mucous skin is quite naked and smooth and devoid of scales. There is no bony skeleton. A very rudimentary skull is developed at the foremost end of their bodies. At this point a soft membranous (partly turning into cartilage), small brain-capsule is formed, and encloses the brain.



Fig. 227.—The lamprey, *Petromyzon fluminalis*, a typical member of the Cyclostoma, showing the single nostril, the rasped mouth, and the ctenoid scales.

The brain of the Cyclostomes is merely a very small and comparatively insignificant swelling of the spinal marrow, a simple vesicle at first. It afterwards divides into five successive cerebral vesicles, like the brain of the Gnathostomes. These five primitive cerebral vesicles, that are found in the embryos of all the higher vertebrates from the fishes to men, and grow into very complex structures, remain at a very rudimentary stage in the Cyclostomes. The histological structure of the nerves is also less advanced than in the rest of the vertebrates. In these the auditory organ always contains three circular canals, but in the larvae there are only two, and in the lampreys only one. In most other respects the organization of the Cyclostomes is much simpler—for instance, in the structure of the heart, circulation, and kidneys. We must especially note the absence of a very important organ that we find in the fishes, the floating bladder, from which the lungs of the higher Vertebrates have been developed.

When we consider all these peculiarities in the structure of the Cyclostomes, we may formulate the following thesis: Two divergent lines proceeded from the earliest Craniota, or the primitive Craniota (*Arthropoda*). One of these lines is preserved in a greatly modified condition: these are the Cyclostomes, a very backward and partly degenerate side-line. The other, the chief line of the Vertebrates itself, advanced straight to the fishes, and by fresh adaptations acquired a number of important improvements.

The Cyclostomes are almost always classified by zoologists among the fishes; but the incorrectness of this may be judged from the fact that in all the chief and distinctive features of organization they are further removed from the fishes than the fishes are from the Mammals, and even man. With the fishes we enter upon the vast division of the jawless.

FIG. 22.—FOSSIL PISCES: *ANTERIOR STAGE OF CYCLOSTOMUS DENTICULATUS*, FROM THE VOLCANIC LAYER OF THE HYDRAE. (From *Zitteliana*.) I. Mouth and buccal musculature;  $\alpha$ , opercular musculature;  $\beta$ , branchial musculature;  $\gamma$ , hypopharyngeal;  $\delta$ , longitudinal;  $\epsilon$ , transverse. II. Vertebrae;  $\alpha$ , anterior;  $\beta$ , middle;  $\gamma$ , posterior. III. Intercarinal cartilage;  $\alpha$ , upper;  $\beta$ , lower. IV. Lateral (lateral) processes;  $\alpha$ , anterior;  $\beta$ , posterior. V. Ventrals;  $\alpha$ , pelvic;  $\beta$ , ventral;  $\gamma$ , ventral pair of organs;  $\delta$ , double pair of organs;  $\epsilon$ , additional supra-anal plates. VI. Anal fin;  $\alpha$ , pelvic;  $\beta$ , ventral;  $\gamma$ , supra-anal organs.



FIG. 22.

or double-nosed Vertebrates (*Gnathostomes* or *Agnathidae*). We have to consider the Salms carefully as the class which, on the evidence of paleontology,

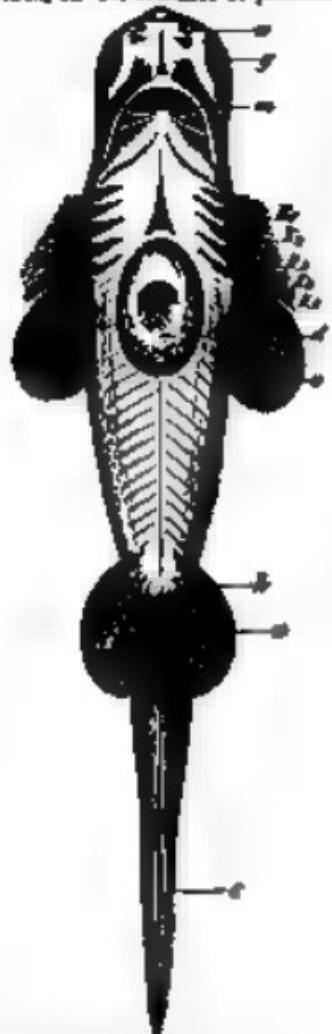


FIG. 292.—Embryo of a shark (*Synanceia* sp.).  
seen from the ventral side.  $\times 10$ . Illustration by James E.  
Perry of photographs by Hollister,  $\times 100$ ,  $\times 1000$ . A  
retouched black-and-white photograph (removed for most part) of  
one,  $\times 1000$ , at monochrome.

comparative anatomy, and entomology, may be regarded with absolute certainty as the

ancestors of all the higher Vertebrates or Gnathostomes. Naturally, none of the actual fishes can be considered the direct ancestor of the higher Vertebrates. But it is certain that all the Vertebrates or Gnathostomes, from the fishes to man, descended from a common, extinct, fish-like ancestor. If we had this ancient stem-fish before us, we would undoubtedly class it as a true fish. Fortunately, the comparative anatomy and classification of the fishes are now so far advanced that we can get a very clear idea of these intermediate and transitional features.

In order to understand properly the systematical tree of our race within the vertebrate stem, it is important to bear in mind the characteristics that separate the tribe of the *Gnathostomes* from the *Cyclostomes* and *Conchozoa*. In these respects the fishes agree entirely with all the other Gnathostomes up to man, and it is on this that we base our claim of relationship to the fishes. The following characteristics of the *Gnathostomes* are distinctive features of this kind: (1) The external gill-slits apparatus with the jaw-arches. (2) The pair of nostrils; (3) the gular bladder or lugs; and (4) the two pairs of lungs.

The peculiar formation of the framework of the branched (gill) arches and the connected maxillary (jaw) apparatus is of importance in the whole group of the Gnathostomes. It is inherent in a rudimentary form by all of them, from the earliest fishes to man. It is true that the primitive transformation (which we find even in the Acanthia) of the fore gut into the branched gut can be traced in all the Vertebrates in the same simple type; in this respect the gill-slits, which pierce the walls of the branched gut in all the Vertebrates and in the Acanthia, are very characteristic. But the external, superficial branchial skeleton that supports the gill-slits in the Cyclostoma is replaced in the Gnathostomes by an internal branched skeleton. It consists of a number of successive cartilaginous arches, which lie in the wall of the gutlet between the gill-slits, and run round the gutlet from both sides. The foremost pair of gill-arches become the maxillary arches, from which we get our upper and lower jaws.

The olfactory organs are at first found in the nose form in all the Graptolites, as a pair of depressions in the fore part of the skin of the head, above the mouth; hence, they are also called the Ambulacrines.

("double-nosed"), The Cyclostomes are "one-nosed" (*Mesostomes*); their nose is a single passage in the middle of the frontal surface. But as the olfactory nerve is double in higher cases, it is possible that the peculiar form of the nose in the actual Cyclostomes is a secondary acquisition (by adaptation to auctorial habits).

A third essential character of the Gnathostomes, that distinguishes them very conspicuously from the lower vertebrates we have dealt with, is the formation of a blind sac by invagination from the fore part of the gut, which becomes in the fishes the Air-filled Floating Bladder. This organ acts as a hydrostatic apparatus, increasing or reducing the specific gravity of the fish by compressing or altering the quantity of air in it. The fish can rise or sink in the water by means of it. This is the organ from which the lungs of the higher vertebrates are developed.

Finally, the fourth character of the Gnathostomes in their simple embryonic form is the two pairs of extremitates or limbs—a pair of fore legs (breast-fins in the fish, Fig. 290 a) and a pair of hind legs (ventral fins in the fish, Fig. 290 b). The comparative anatomy of these fins is very interesting, because they contain the rudiments of all the skeletal parts that form the framework of the fore and hind legs in all the higher vertebrates right up to man. There is no trace of these pairs of limbs in the Acanthines and Cyclostomes.

Turning now to a closer inspection of the fish class, we may first divide it into three groups or sub-classes, the genealogy of which is well known to us. The first and oldest group is the sub-class of the *Selachii* or primitive fishes, the best-known representatives of which to-day are the orders of the sharks and rays (Figs. 292-292). Next to this is the more advanced sub-class of the plated fishes or *Gymnoids* (Figs. 293-5). It has been long extinct for the most part, and has very few living representatives, such as the sturgeons and the bony pike; but we can form some idea of the earlier extent of this interesting group from the large numbers of fossils. From these plated fishes the sub-class of the bony fishes



Fig. 292.—Fully developed embryo of a shark (*Carcharodon carcharias*). After Haeckel, modified after Gegenbaur, and drawn by W. K. Parker.

or *Telostei* was developed, to which the great majority of living fishes belong (especially nearly all our river fishes). Comparative anatomy and ontogeny show clearly that the Gnathida descended from the Selachii, and the Teleostei from the Gnathida. On the other hand, a collateral



The figure represents a fossil fish, *Gnathodus*, from the Upper Silurian of Belgium. Above, the anterior end; below, the middle part of the body, and the posterior end. The scale bar indicates one inch. Between these two parts, there is a number of inches.

line, or rather the advancing chief line of the vertebrate stem, was developed from the earlier Gnathida, and this leads us through the group of the Diplopeltini to the important division of the Actinopterygii.

The earliest fossil remains of Vertebrates that we know were found in the

Upper Silurian (p. 302), and belong to two groups—the Selachii and the Gnathida. The most primitive of all known representatives of the earliest fishes are probably the remarkable *Pteraspis* (Fig. 292), the genera *Phenacanthus*, *Nemacanthus*, *Orthacanthus*, etc. (Fig. 293). These ancient cartilaginous fishes agree in most points of structure with the real sharks (Figs. 292, 293); but in other respects they seem to be no more simple in organization than many palaeontologists separate them altogether, and regard them as *Proselachii*; they are probably closely related to the earliest ancestors of the Gnathostomes. We find well-preserved remains of them in the Permian period. Well-preserved impressions of older sharks are found in the Jurassic strata, such as of the angel-shark (*Squatina*, Fig. 294). Among the earliest marine sharks of the Tertiary period there were some twice as large as the biggest living fishes; *Carcharodon* was more than 100 feet long. The sole surviving species of this genus (*C. limbatus*) is eleven yards long, and has teeth two inches long; but among the fossil species we find teeth six inches long (Fig. 295).

From the primitive fishes or Selachii, the earliest Gnathostomes, was developed the begin of the Gnathida. There are very few groups now of this interesting and varied group—the ancient sturgeons (*Acipenser*), the eggs of which are eaten as caviare, and the small oil fishes (*Polypterus*, Fig. 296) in African rivers, and the oil fishes (*Lampris*, Fig. 297) in the rivers of North America. On the other hand, we have a great variety of specimens of this group in the fossil state, from the Upper Silurian onward. Some of these fossil Gnathida approach closely to the Selachii; others are closer to the Diplopeltini; others again represent a transition to the Teleostei. For our genealogical purposes the most interesting are the intermediate forms between the Selachii and the Diplopeltini. Blassey, to whom we owe particularly important studies on the fossil Gnathida, classed them in the order of the *Crossopterygii*. Many genera and species of this order are found in the Devonian and Carboniferous strata (Fig. 298); a single, greatly modified survivor of the group is still found in the large rivers of Africa (*Polypterus*, Fig. 296), and the closely related *Catostomidae*. Numerous impressions of the Crossopterygii, the "flying bladders" seems to be oxidized,

and therefore well  
in the *Undas* (—  
behind the head).

Part of these *Crossopterygii*,  
very closely in their chief division,  
to the Dipneusts, and thus represent phy-  
logenetically the transition from the  
Devonian Crossopterygii to the earliest air-  
breathing vertebrates. This important  
advance was made in the Devonian  
period. The numerous fossils that we

have at the first two geological

the Laurentian and Cambrian periods,  
belong exclusively to aquatic plants and  
animals. From this paleontological fact,  
in conjunction with important geological  
and biological indications, we may  
infer with some confidence that  
there were no terrestrial animals  
at that time. During the whole  
of the vast archæan period—  
many millions of years—the living  
population of our planet consisted  
almost exclusively of aquatic organisms.  
This is a very remarkable  
fact, when we remember that this  
period embraces the larger half of  
the whole history of life. The lower  
animal-stems are wholly (or with  
very few exceptions) aquatic. But  
the higher stems also remained in  
the water during the primordial  
epoch. It was only towards its close  
that some of them came to live on  
land. We find isolated fossil remains  
of terrestrial animals first in the  
Upper Silurian, and in larger  
numbers in the Devonian strata,  
which were deposited at the begin-  
ning of the second chief series—  
geology (the paleozoic age). The  
number increased rapidly  
in the Carboniferous and Permian  
deposits. We find many species  
both of the articulate and the vertebrate

on land and breathed the  
atmosphere; their aquatic ancestors of  
the Silurian period only breathed water.  
This important change in respiration is  
the chief modification that the animal  
organism underwent in passing from the  
water to the solid land. The first  
step was the formation of lungs for  
breathing air; up to that time the gills  
alone had served for respiration. But  
there was at the same time a great  
change in the circulation and its organs;  
these are always very closely correlated to  
the respiratory organs. Moreover, the  
limbs and other organs were also much

or less modified, either in consequence of  
remote correlation to the preceding or  
owing to new adaptations.

In the vertebral stem it was unquestionably a branch of the fishes—in fact, of  
the Crossopterygii—that made the first fortunate  
expedition, during the Devonian period  
of adapting themselves to terrestrial life  
and breathing the atmosphere. This  
is a modification of the heart and the

lungs. The true fishes have merely a pair  
of blind olfactory pits on the surface  
of the head; but a connection of these with  
the cavity of the mouth was now formed.  
A canal made its appearance on each side,  
and led directly from the nasal depression



FIG. 22.—Snout of a sturgeonshark (*Ctenacanthus*) from the Palaeozoic rocks of West Virginia (see text).

into the mouth-cavity,  
atmospheric air to the  
blood. Further, in all  
true fishes the heart has only two sections  
—an atrium that receives the venous  
blood from the veins, and a ventricle  
that propels it through a conical artery  
to the gills; the atrium was now divided  
into two halves, or right and left auricles,  
by an incomplete partition. The right  
auricle alone now received the venous  
blood from the body, while the left auricle  
received the venous blood that flowed  
from the lungs and gills to the heart.  
Thus the double circulation of the higher  
vertebrates was evolved from the simple

circulation of the true fishes, and, in accordance with the laws of evolution, this advance led to changes in the structure of other organs.

The vertebrate class, that then adopted

they retained the earlier gill-respiration along with the new pulmonary (lung) respiration, till the lowest Amphiibia. This class was represented during the paleozoic age (or the Devonian, Car-

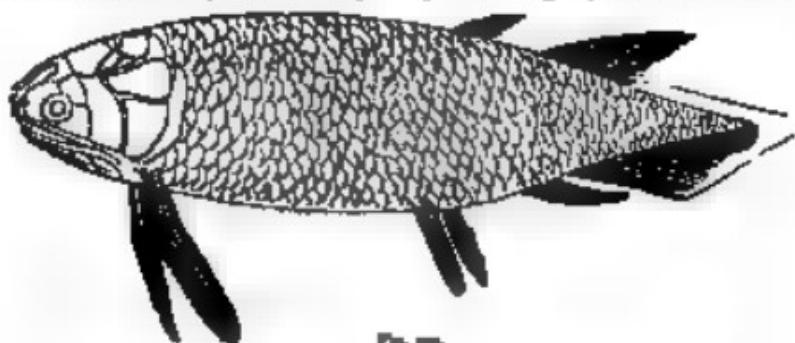


FIG. 323.

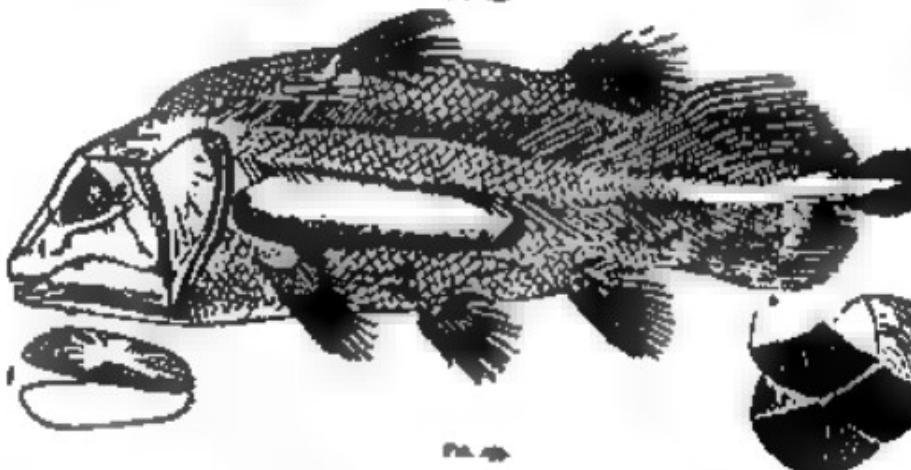


FIG. 324.



FIG. 325.

FIG. 323.—A Devonian Craniostylogaster (*Hindichthys*) from the Lower Silurian of New York.

FIG. 324.—A Devonian Craniostylogaster (*Undina* gen. nov.), from the Lower Silurian of New York.

FIG. 325.—A living Craniostylogaster, from the Upper Lake of Polyphemus Inlet, New York.

itself to breathing the atmosphere, and was developed from a branch—*Gnathostoma*, takes the name of the *Diplopeltis* or *Dipaea* ("double-breathers"), because

homologous, and *Perciformes*. A number of different genera, only three genera of the *Diplopeltis* exist today: *Ptychopterus* contains

of tropical Africa (the White Nile, the Niger, Quelidion, etc.), *Zeophorus paradoxus* in tropical South America (in the tributaries of the Amazon), and *Ceratodus Forsteri* in the rivers of East Australia. This wide distribution of the three isolated survivors proves that they represent a group that was formerly very large. In their whole structure they

entirely now associate them with the fishes. As a matter of fact, the characters of the two classes are so far united in the Diplopeltis that the answer to the question depends entirely on the definition we give of "fish" and "amphibian." In habits they are true amphibia. During the tropical winter, in the rainy season, they swim in the water like the fishes; and

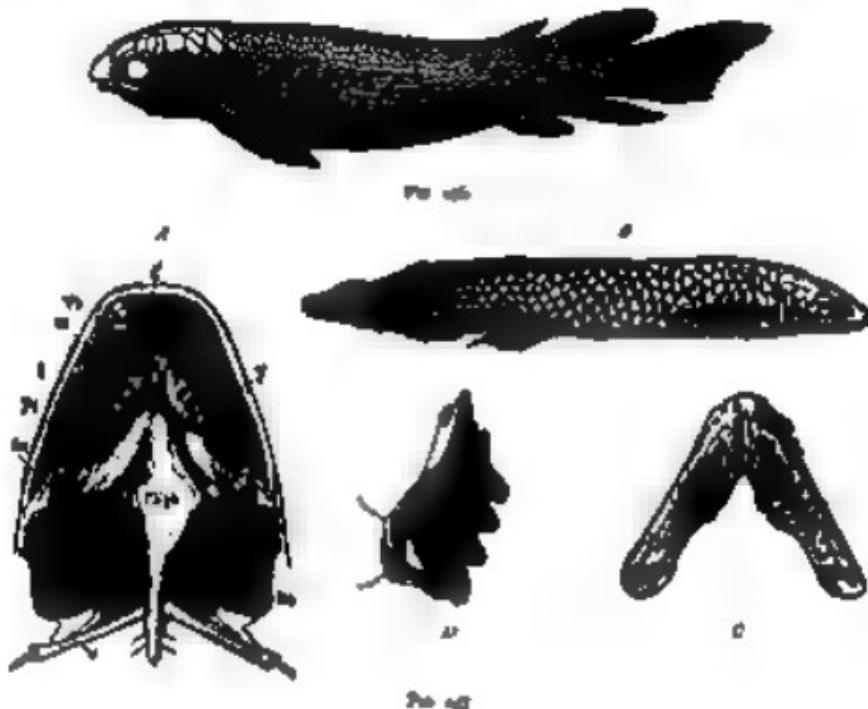


FIG. 436.—*Diplopeltis (Ceratodus Forsteri)*, *sp.* from the Old Red sandstone (Devon). (From Pander.) FIG. 437.—The Australian Diplopeltis (*Ceratodus Forsteri*). *sp.* from the Old Red sandstone, *sp.* from the Devon. *A*, lateral view; *B*, ventral view; *C*, head; *D*, anterior part; *E*, posterior part. *A* and *B*, *C* and *D*, *E*, *enlarged*. (See also *Fig. 438*.) (From the Trans.)

form a transition from the fishes to the amphibia. The transposed formation between the two classes is so pronounced in the whole organization of these remarkable animals that zoologists had a lively controversy over the question whether they were really fishes or amphibia. Several distinguished naturalists classed them with the amphibia,

breathing water by gills. During the dry season, they bury themselves in the dry sand, and breathe the atmosphere through lungs, like the amphibia and the higher vertebrates. In this double respiration they resemble the lower amphibia, and have the same characteristic formation of the heart; in this they are much superior to the fishes. But in most other features

they approach nearest to the fishes, and are inferior to the arachthids. Internally they are entirely fish-like.

In the Dipneusti the head is not marked off from the trunk. The skin is covered with large scales. The pharynx is soft, cartilaginous, and at a low stage of development, as in the lowest Selachii and the earliest Ganoids. The heart is completely retained, and surrounded by an unsegmented sheath. The two pairs of lungs are very simple fleshy structures.

skeleton; the cartilaginous skeleton of its two pairs of fins, for instance, has still the original form of a bi-serial or feathered leaf, and was on that account described by Gegenbaur as a "primitive fin-skeleton." On the other hand, the skeleton of the pair of fins is greatly reduced in the African dipneust (*Propterus*) and the American (*Lepidosteus*). Further, the lungs are double in these modern dipneusts, as in all the other air-breathing vertebrates; they



FIG. 48.



FIG. 49.

FIG. 48.—Young coelacanth, shortly after coming from the egg, magnified six times. (After Gegenbaur.) FIG. 49.—Young coelacanth, no earlier than coming from the egg, a typical fish of gen. 1 reduplicating teleost. (After Richard Owen.)

type, like those of the lowest Selachii. The formation of the brain, the gut, and the sexual organs is also the same as in the Selachii. Thus the Dipneusti have preserved by heredity many of the less advanced features of our primitive fish-like ancestors, and at the same time have made a great step forward in adaptation to air-breathing by means of lungs and the concomitant improvement of the heart.

*Ceratodus* is particularly interesting on account of the primitive build of its

lungs on that account been called "double-branched" (*Dipneustes*) in contrast to the Ceratodontidae; the latter has only a single lung (*Muraenesomidae*). At the same time the gills also are developed as water-breathing organs in all these lung-fishes. *Propterus* has external as well as internal gills.

The paleozoic Dipneusti that are in the direct line of our ancestry, and form the connecting-links between the Ganoids and the Amphilophids, differ in many respects

from their living descendants, but agree with them in the above essential features. This is confirmed by a number of interesting facts that have lately come to our knowledge in connection with the

embryonic development of the Ceratodus and Diplocaulus; they give us important information as to the stem-history of the lower Vertebrates, and therefore of our early ancestors of the palaeozoic age.

## CHAPTER XXII.

### OUR FIVE-TOED ANCESTORS

WHEN the phylogenetic study of the four higher classes of Vertebrates, which must now engage our attention, we reach much firmer ground and more light in the construction of our genealogy than we have, perhaps, enjoyed up to the present. In the first place, we owe a number of very valuable data to the very interesting class of Vertebrates that come next to the Dipneusts and have been developed from them—the Amphibia. To this group belong the salamander, the frog, and the toad. In earlier days all the reptiles were, on the example of Linnaeus, classed with the Amphibia (lizards, serpents, crocodiles, and tortoises). But the reptiles are much more advanced than the Amphibia, and are nearer to the birds in the chief points of their structure. The true Amphibia are nearer to the Dipneusts and the fishes; they are also much older than the reptiles. There were plenty of highly-developed (and sometimes large) Amphibia during the Carboniferous Period; but the earliest reptiles are only found in the Permian period. It is probable that the Amphibia were evolved even earlier—during the Devonian period—from the Dipneusts. The extinct Archamphibia of which we have fossil remains from that remote period (very numerous especially in the Triassic strata) were distinguished for a graceful body and a powerful locomotion on the land (like the crocodile), whereas the living amphibia have usually a smooth and slippery skin.

The earliest of these ancestral Amphibia (*Pterospondylus*) form the order of *Stereophylidae* ("root-banded") (Fig. 560). It is among these, and not among the actual Amphibia, that we must look for the forms that are closely related to the genealogy of man; and are the ancestors of the three higher

classes of Vertebrates. But even the existing Amphibia have such important relations to us in their anatomic structure, and especially their embryonic development, that we may say: Between the Dipneusts and the Amphibia there was a series of extinct intermediate forms which we should certainly class with the Amphibia if we had them before us. In their whole organization over the actual Amphibia seem to be an instructive transitional group. In the important respects of respiration and circulation they approach very closely to the Dipneusts, though in other respects they are far superior to them.

This is particularly true of the development of their limbs or extremities. In them we find them for the first time as five-toed feet. The thorough investigations of Gegenbaur have shown that the fish's fin, of which very erroneous opinions were formerly held, are many-toed feet. The radialis carpalis or bowy radii that are found in large numbers in each fin correspond to the fingers or toes of the higher Vertebrates. The intercalary joints of each fin-radius correspond to the various parts of the toe. Even in the Dipneusts the fin is of the same construction as in the fishes; it was afterwards gradually evolved into the five-toed form, which we first encounter in the Amphibia. This reduction of the number of the toes to six, and then to five, probably took place in the second half of the Devonian period—at the latest, in the subsequent Carboniferous period—in those Dipneusts which we regard as the ancestors of the Amphibia. We have several fossil remains of five-toed Amphibia from this period. There are skeletons of fossil amphibia of them in the Triassic of Thuringia (*Clethroidium*).

The fact that the fore-toe number five is of great importance, because they have clearly been transmitted from the Amphibia to all the higher Vertebrates. Man entirely abandons his amphibia-

It is well known that this hereditary number of the toes has assumed a very great practical importance from remote times; e.g. in our whole system of enumeration (the decimal system applied to estima-



FIG. 10.—FROG skeleton from the Papposaurus. Found in the Wissous terrane near Dresden (Mitteldeutsche Kreide). (From Gmelin.) A division of a young larva. A larva, restored, with gills. C the skull form, dorsal view.

ancestors in this respect, and indeed in the whole structure of the body skeleton of his five-toed extremities. A careful comparison of the skeleton of the frog with our own is enough to show this. It

most of time, shape, weight, etc.) is based. There is absolutely no reason why there should be five toes in the fore and hind feet in the lowest Amphibia, the reptiles, and the higher Vertebrates, unless we

scribe it to inheritance from a common stem-form. Heredity alone can explain it. It is true that we find less than five toes in many of the Amphibia and of the higher Vertebrates. But in all these cases we can prove that some of the toes atrophied, and were in time lost altogether.

The cause of this evolution of the five-toed foot from the many-toed fin in the amphibian ancestor must be sought in adaptation to the entire change of function that the limbs experienced in passing from an exclusively aquatic to a partly terrestrial life. The many-toed fin had been used almost solely for respiration in the water; it had now also to support the body in creeping on the solid ground. This led to a modification both of the skeleton and the muscles of the limbs. The number of the fin-rays was gradually reduced, and sank finally to five. But those five remaining rays became much stronger. The soft cartilaginous rays became bony rods. The rest of the skeleton was similarly strengthened. Thus from the one-armed fins of the many-toed fish-fin arose the improved many-armed lever system of the five-toed amphibian limbs. The movements of the body gained in variety as well as in strength. The various parts of the skeletal system and correlated muscular system began to differentiate more and more. In view of the close correlation of the muscular and nervous systems, this also made great advance in structure and function. Hence we find, as a matter of fact, that the brain is much more developed in the higher Amphibia than in the fishes, the Dipneusts, and the lower Amphibia.

The first advance in organization that was occasioned by the adoption of life on land was naturally the construction of an organ for breathing air—a lung. This was formed directly from the lung-bladder inherited from the fishes. At first its function was inconvenient beside that of the gills, the older organ for water-respiration. Hence we find in the lowest Amphibia, the gilled Amphibia, that, like the Dipneusts, they pass the greater part of their life in the water, and breathe water through gills. They only come to the surface at brief intervals, or creep out to the land, and then breathe air by their lungs. But some of the so-called Amphibia—the salamanders—remain entirely in the water when they are young, and afterwards spend most of their time on

land. In the adult state they only breathe air through lungs. The same applies to the most advanced of the Amphibia, the Batrachia (frogs and toads); some of these have entirely lost the gill-bearing larva form.<sup>1</sup> This is also the case with certain small, serpentine Amphibia, the Caecilia (which live in the ground like earth-worms).

The great interest of the natural history of the Amphibia consists especially in their intermediate position between the lower and higher Vertebrates. The lower Amphibia approach very closely to the



The larva of the typical Salamander (Salamandra salamandra), seen from the ventral side. In the center a single pair of legs from the front. The external gills are specially indicated. The two pairs of legs are still very small.

Dipneusta. In their whole organization, like mainly in the water, and breathe by gills; but the higher Amphibia are just as close to the Amniotes, live mainly on land, and breathe by lungs. But in their younger state the latter resemble the former, and only reach the higher stage by a complete metamorphosis. The embryonic development of most of the

<sup>1</sup> The young of Rana temporaria (*Rana temporaria*) have the gills on the outside, and the tail and yolk-sac on the outside, too, of their body. On the mouth or mouth-day after hatching the frog emerges from the egg.

higher Amphibia still faithfully reproduces the stem-history of the whole class, and the various stages of the evolution that was made by the lower Vertebrates in passing from aquatic to terrestrial life during the Devonian or the Carboniferous period are repeated in the spring by every frog that develops from an egg in our ponds.

The common frog leaves the egg in the shape of a larva, like the tailless salamander (Fig. 361), and this is altogether different



The an-larva of the common frog (Rana temporaria), or "tadpole," as it is called, is a larva of striking contrast to others of similar form, such as the pleuronectes. Below is the gill-cleft, from which the branching gills (3) project, a bell-shaped, cutaneous foldings of the tail.

from the mature frog (Fig. 362). The short trunk ends in a long tail, with the form and structure of a fish's tail (2). There are no limbs at first. The respiration is exclusively branchial, first through external (3) and then internal gills. In harmony with this the heart has the same structure as in the fish, and consists of two sections—an atrium that receives the venous blood from the body, and a ventricle that forces it through the aorta into the gills.

We find the larva of the frog (or tadpole, *Gymnophion*) in great numbers in our ponds every spring in this fish-form, using their muscular tails in swimming, just like the fishes and young Ascidia. When they have reached a certain size, the remarkable metamorphosis from the fish-form to the frog begins. A blind sac grows out of the gut, and expands into a couple of spacious ones: these are the lungs. The simple chamber of the heart is divided into two sections by the development of a partition, and there are at the same time considerable changes in the structure of the chief arteries. Previously all the blood went from the auricle through the aortic arches into the gills, but now only part of it goes to the gills, the other part passing to the lungs through the new-formed pulmonary artery. From this point arterial blood returns to the left auricle of the heart, while the venous blood gathers in the right auricle. As both auricles open into a single ventricle, this contains mixed blood. The diminutive form has now succeeded to the fish-form. In the further course of the metamorphosis the gills and the branchial vessels entirely disappear, and the respiration becomes exclusively pulmonary. Later, the long swimming tail is lost, and the frog now hops to the land with the legs that have grown meantime.

This remarkable metamorphosis of the Amphibia is very instructive in connection with our human genealogy, and is particularly interesting from the fact that the various groups of adult Amphibia have remained at different stages of their stem-history, in harmony with the biogeographic law. We have first of all a very low order of Amphibia—the Gymnophiones ("gilled-amphibians"), which retain their gills throughout life, like the fishes. In a second order of the salamanders the gills are lost in the metamorphic, and when fully grown they have only pulmonary respiration. Some of the naked Amphibia still retain the gill-clefts in the side of the neck, though they have lost the gills themselves (*Aneides*). If we force the larvae of our salamanders (Fig. 363) and urtires to remain in the water, and prevent them from reaching the land, we can in favourable circumstances make them retain their gills. In this fish-like condition they reach sexual maturity, and remain throughout life at the lower stage of the gilled Amphibia.

We have the reverse of this experiment. In a Mexican gilled salamander, the fish-like axolotl (*Salmon pachneri*), it was formerly regarded as a permanent gilled amphibian persisting throughout life at the fish-stage. But some of the hundreds of these animals that are kept in the Botanical Garden at Paris get on to the land for some reason or other, lose their gills, and change into a form closely resembling the salamander (*desmognathus*). Other species of the genus become sexually mature for the first time in this condition. This has been regarded as an astounding phenomenon, although every common frog and salamander repeats the metamorphosis in the spring. The whole change from the aquatic and lung-breathing animal to the terrestrial lung-breathing form may be followed step by step in the case. But what we

Their ancestors also had long tails and gills like the gilled Amphibia, as the tail and the gillarches of the human embryo clearly show.

For comparative anatomical and ontogenetic reasons, we must not seek these amphibian ancestors of ours—as one would be inclined to do, perhaps—among the tail-less Batrachia, but among the tailless Lower Amphibia.

The vertebrate form that comes next to the Amphibia in the series of our ancestors is a lizard-like animal, the earlier existence of which can be confidently deduced from the facts of comparative anatomy and ontogeny. The living *Ahaeus* of New Zealand (Fig. 244) and the extinct *Plymognathus* of the Permian period (Fig. 245) are closely related to this important stem-form; we may call them the *Primitivores*, or *Primitive Amniotes*.



Fig. 244.—Small modern amniote, from the Victorian Coal-fields (Ahaeus). (From Pröbst.) The body and tail related to the head.

we find in the development of the individual has happened to the whole class in the course of its stem-history.

The metamorphosis goes further in a third order of Amphibia, the *Heterodermia* or *Anura*, than in the salamander. To this belong the various kinds of frogs, fringed salamanders, water-frogs, tree-frogs, etc. These lose, not only the gills, but also (sooner or later) the tail, during metamorphosis.

The ontogenetic loss of the gills and the tail in the frog and toad can only be explained on the assumption that they are descended from long-tailed Amphibia of the salamander type. This is also clear from the comparative anatomy of the two groups. This remarkable metamorphosis is, however, also interesting because it throws a certain light on the phylogeny of the tailless types—

All the Vertebrates above the Amphibia—or the three classes of reptiles, birds, and mammals—differ so much in their whole organization from all the lower Vertebrates we have yet considered, and bear so great a resemblance to each other, that we put them all together in a single group with the title of *Amniota*. In these three classes alone we find the remarkable amniotic membrane, already mentioned, which we called the *anserine* or *convergenticistic* adaptation that we may regard as a result of the sinking of the growing embryo into the yolk-sac.

All the Amniotes known to us—all reptiles, birds, and mammals (including man)—agree in so many important points of internal structure and development that their descent from a common ancestor can be affirmed with tolerable certainty. If the evidence of comparative

embryology and ontogeny is over entirely beyond question, it is certainly the same here. All the peculiarities that distinguish, and follow the formation of the Amniote, and that we have interest in our consideration of human embryology; all the peculiarities in the development of the organs which we shall probably follow in detail, finally, all the principal special features of the internal structure of the All-green Amniotes—prove positively the common origin of all the Amniotes from a single aiternal ancestor; that it is difficult to ascertain the size of their ancestors from several independent groups of unknown common ancestry, in our Primitive Amniote (*Pterosphenus*). In outward appearance it was probably something between the teleostean and the Nect.

It is very probable that some part of the Permian period was the age of the origin of the Pterosphenids. That follows from the fact that the Amniotic era are fully developed even the Carboniferous period, and that the first fossil record (*Pterosphenus*, *Amphibolites*, *Pholidoscelis*, etc.) are found towards the close of the Permian period. Among the important changes of the vertebrate organization that marked the rise of the first Amniotes from teleostean ancestors during this period the following were especially noteworthy: the early differentiation of the water-breathing gills and the conversion of the gill-circles into air-tubes, the formation of the oesophagus, the primitive urinary sac, and the development of the coelom.

One of the most salient characteristics of the Amniote is the complete loss of the gills. All Amniotes, in contrast to other fish (such as sea-scorpions and whalefish), breathe air through lungs, never water through gills. All the Amniotes (with very rare exceptions) retain their gills for many days when young, and have lost a time (but permanently) branchial respiration. Not after these there is no question of branchial respiration. The Pterosphenids must have entirely abandoned water-breathing. Nevertheless, the gill-circles are preserved by heredity, and develop into totally different (in part respiratory) organs—various parts of the base of the tongue, the floor of the jaw, the crypts of Barany, etc. But we do not find in the embryo of the Amniote any trace of gills, either, or of any respiratory organs in the gill-circles.

With this complete abandonment of the gills is probably connected the formation of another organ, to which we have already referred in embryology—namely, the pharynx, or primitive larynx (see p. 482). It is very probable that the primary bladder of the Diplopoda is the first structure of the pharynx. We find in there a primary bladder that proceeds from the lower wall of the head and of the gut, and serves as receptacle for the oral mucous. This organ has been transmitted to the Amniotes, it is said as in the frog.

The formation of the coelom and the allantois and the complete disappearance of the gills are the chief characteristics distinguishing the Amniotes from the lower Vertebrates we have hitherto considered. To these we may add several characteristics features that are distributed to all the Amniotes, and are found in them only. One striking peculiarity character of the Amniote is the great curve of the head and neck in the embryo. We also find an advance in the structure of several of the internal organs of the Amniotes which raises them above the higher of the teleostean. In particular, a portion is formed in the simple mouth of the heart, divided into right and left chambers. In addition while the complete regeneration of the gill-circles we find a further development of the respiratory organs. Also, there is a great advance in the structure of the brain, skeleton, muscular system, and other parts. Finally, one of the most important changes is the development of the kidneys. In all the earlier Vertebrates we have found the primitive kidneys, or Malpighian organs, and these appear at an early stage in the history of all the higher Vertebrates up to man. But in the Amniotes these primitive kidneys cease to act at an early stage of vertebrate life, and their function is taken up by the permanent or secondary kidneys, which develop from the terminal part of the present ducts.

Taking all these peculiarities of the Amniote together, it is impossible to doubt that all the members of this group—captive birds, and mammals—have a common origin, and form a singly blood-related stem. Our next task belongs to this stem. Here is in every feature of his organization and undergoing development, a type common, and has descended from the Pterosphenus with all the other

**Ammiates.** Though they appeared at the end (possibly even in the middle) of the Palaeozoic age, the Ammiates only reached their full development during the Mesozoic age. The birds and mammals made their first appearance during this period. Even the reptiles show their greatest growth at this time, so that it is called "the reptile age." The extinct Protomammal, the ancestor of the whole group,

and only comes in contact with the Mammals at its root; is the combined group of the reptiles and birds; these two classes may, with Huxley, be conveniently grouped together as the Sauropsida. Their common stem-form is an ancient lizard-like reptile of the order of the Rhynchosauria. From this have been developed in various directions the saurians, crocodiles, tortoises, etc.—in a



To the left—The Head of *Micromelerpeton gracilis* (Sauvage) of New Zealand. The male mounting specimen (Prestwich)

belongs in its whole organization to the reptile class.

The genealogical tree of the saurian group is clearly indicated in its chief lines by their paleontology, comparative anatomy, and ontogeny. The group succeeding the Protomammal divided into two branches. The branch that will claim our whole interest is the class of the Mammals. The other branch, which developed in a totally different direction,

word, all the members of the reptile class, but the remarkable class of the birds has also been evolved directly from a branch of the reptile group, as is now established beyond question. The embryos of the reptiles and birds are identical until a very late stage, and have an astonishing resemblance even later. Their whole structure agrees so much that no anatomist now questions the descent of the birds from the reptiles. On the other

head, the mammal line has descended from the group of the Sauromammalia, a different branch of the Proteropoda. It is connected at its deepest roots with the reptile line, but it then diverges completely from it and follows a distinctive development. Man is the highest outcome of this class, the "crown of creation." The hypothesis that the three higher Vertebrate classes represent a single Amniote stem, and that the common root of this stem is to be found in the amphibian class, is now generally admitted.

The instructive group of the Permian Theroherpetia, the common root from which the divergent stems of the Sauropoda and mammals have issued, merits our particular attention as the stem-group of all the Amniotes. Fortunately a living representative of this cohort survived

right), of which well-preserved skeletons are found in the Solnhofen shales, is perhaps still more closely related to them.

Unfortunately, the numerous fossil remains of Permian and Triassic Theroherpetia that we have found in the last two decades are, for the most part, very imperfectly preserved. Very often we can make only precarious inferences from these skeletal fragments as to the anatomic characters of the soft parts that went with the bony skeleton of the extinct Theroherpetia. Hence it has not yet been possible to arrange these important fossils with any confidence in the ancestral series that descend from the Proteropoda to the Sauropoda on the one side and the Mammals on the other. Opinions are particularly divided as to the place in classification and the phylogenetic significance of the remarkable Theromorphia



FIG. 246.—*Diadectes pectoralis*, a large synapsid from Kataldo. (From Zittel.)

group has been preserved to our day: this is the remarkable Board of New Zealand, *Hedbergia punctata* (Fig. 264). Externally it differs little from the ordinary lizard; but in many important points of internal structure, especially in the primitive construction of the vertebral column, the skull, and the limb, it occupies a much lower position, and approaches its amphibian ancestors, the Stegocephala. Hence *Hedbergia* is the phylogenetically oldest of all living reptiles, an isolated survivor from the Permian period, closely resembling the common ancestor of the Amniotes. It must differ so little from this extinct form, our hypothetical Protosynapsid, that we put it next to the Proteropoda. The remarkable Permian *Paleothyris*, that Cope described in the Platten terrane at Dresden in 1866, belongs to the same group (Fig. 265). The Jurassic genus *Amphibolites* (Fig.

Cope) gives this name to a very interesting and extensive group of ancient terrestrial reptiles, of which we have only fossil remains from the Permian and Triassic strata. Forty years ago some of these Theroherpetia (fresh-water animals) were described by Owen as *Ammobrotis*. But during the last twenty years the distinguished American paleontologists, Cope and Osborn, have greatly increased our knowledge of them, and have claimed that the stem-forms of the Mammals must be sought in this order. As a matter of fact, the Theromorphia are closer to the Mammals in the chief points of structure than any other reptiles. This is especially true of the Theroherpetia, to which the *Pterosaurus* and *Polydactylus* belong (Fig. 267). The whole structure of their pelvis and hind-foot has retained the same form as in the Monotremes, the lowest Mammals. The formation of the

scapula and the quadrato-vomer shows an approach to the Mammals such as we find in no other group of reptiles. The teeth also are already divided into incisors, canines, and molars. Nevertheless, it is very doubtful whether the Therapsidae really are in the ancestral line of the Sauromammalia, or lead direct from the Ticosisauria to the earliest Mammals. Other experts on this group believe that it is an independent lineage of the reptiles, connected, perhaps, at its lowest root, with the Sauromammalia, but developed quite independently of the Mammals—though parallel to them in many ways.

One of the most important of the ecological facts that we rely on in our investigation of the genealogy of the Human race is the position of man in the Mammal class. However different the view of zoologists may have been as to this position in detail, and as to his relation to the apes, no scientist has ever doubted that man is a true mammal in his whole organization and development. Linnaeus alludes to this fact in the first edition of his famous *Systema Naturae* (1735). As will be seen in any museum of anatomy or any manual of comparative anatomy, the human frame has all the characteristics that are common to the Mammals and distinguish them conspicuously from all other animals.

If we examine this undoubted fact from the point of view of phylogeny, in the light of the theory of descent, it follows at once that man is of a common stem with all the other Mammals, and comes from the same root as they. The various features in which the Mammals agree and by which they are distinguished are of such a character as to make a polyphyletic hypothesis quite impossible. It is impossible to entertain the idea that all the living and extinct Mammals come from a number of separate roots. If we accept the general theory of evolution, we are bound to admit the monophyletic hypothesis of the descent of all the Mammals (including man) from a single mammalian stem-form. We may call this long extinct root-form and its earliest descendants (a few genera of one family) "primitive mammals" or "stomamimals" (*Stomamammalia*). As we

have already seen, this root-form developed from the primitive Proterolepis stem in a totally different direction from the Birds, and soon separated from the main stem of the reptiles. The differences between the Mammals and the reptiles and birds are so important and characteristic that we can assume with complete confidence this division of the vertebrates at the commencement of the development of the Amniotes. The reptiles and birds, which we group together as the *Sauropsidae*, generally agree in the characteristic structure of the skull and brain, and this is notably different from that of the Mammals. In most of the reptiles and birds the skull is connected with the first cervical vertebra (the *occiput*)



PL. XII.—Skull of a Pachysaurs lizard (*Archosaurus latifrons*), a small form of basal archosaurian, a generalized form, as contrasted with the advanced forms, as represented.

by a single, and in the Mammals (and Amniotes) by a double, condyle at the back of the head. In the former the lower jaw is composed of several pieces, and connected with the skull so that it can move by a special maxillary bone (the *quadrate*); in the Mammals the lower jaw consists of one pair of bony pieces, which articulate directly with the temporal bone. Further, in the Sauropsidae the skin is clothed with scales or feathers; in the Mammals with hair. The red blood-cells of the former have a nucleus; those of the latter have not. In fine, two quite characteristic features of the Mammals, which distinguish them not only from the birds and reptiles, but from all other animals, are the possession of a

complete diaphragm and of mammary glands that produce the milk for the nutrition of the young. It is only in the Mammals that the diaphragm forms a transverse partition of the body-cavity, completely separating the thoracic from the abdominal cavity. It is only in the mammals that the mother suckles her young, and this rightly gives the name to the whole class (mamma = breast).

From these apparent facts of comparative anatomy and ontogeny it follows absolutely that the whole of the Mammals belong to a single natural stem, which

and the teeth; (3) the development of a hairy coat; (4) the complete formation of the diaphragm; and (5) the construction of the mammary glands and adaptation to suckling. Other important changes of structure proceeded step by step with these.

The epoch at which these important advances were made, and the foundation of the Mammal class laid, may be put with great probability in the first section of the Mesozoic or secondary age—the Triassic period. The oldest fossil remains of mammals that we know were found in strata that belong to the earliest Triassic period—the upper Keuper. One of the earliest forms is the genus *Drimotherium*, from the North American Trias (Fig. 52). Their teeth still strongly recall those of the Polyopisthia. Hence we may assume that this small and probably lowly organized mammal belonged to the stem-group of the Thiomammalia. We do not find any positive trace of the third and most advanced division of the Mammal—the Plesiomammia. These (including man) are much younger, and we do not find indisputable fossil remains of them until the Cenozoic age, or the Tertiary period.

This paleontological fact is very important, because it fully harmonizes with the evolutionary succession of the Mammal orders that is deduced from their comparative anatomy and ontogeny. The latter science teaches us that the whole Mammal class divides into three main groups or sub-classes, which correspond to three successive phylogenetic stages. These stages, which also represent three important stages in our human genealogy, were first distinguished in 1816 by the eminent French naturalist, Blanville, and received the names of *Oligotrichia*, *Hediphiia*, and *Mesotrichia*, according to the construction of the female organs (oligotrichia = uterus or womb). Husley afterwards gave them the names of *Pseudatheria*, *Metatheria*, and *Aetheria*. But the three sub-classes differ so widely from each other, not only in the construction of the sexual organs, but in many other respects also, that we may confidently draw up the following

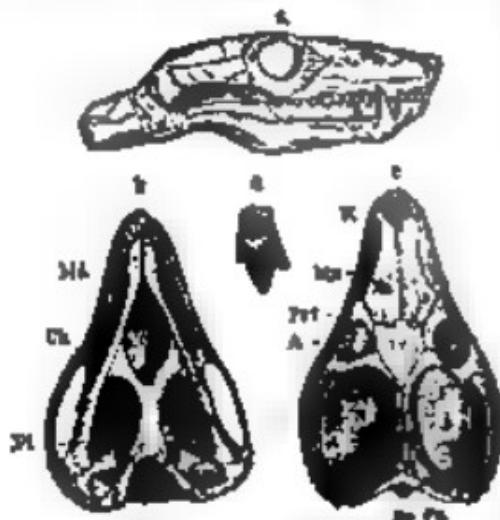


FIG. 52.—Skull of a Triassic Mammal (genus *Drimotherium*) from the Lower Keuper in South Africa. From Owyang's *Fossils* from the right, & front teeth. *a*, Upper teeth of *Drimotherium*; *b*, molar; *c*, upper incisor. *Dx*, front teeth; *Mx*, molars; *Tet.*, upper premolars; *A.*, upper canines; *Pm*, lower premolars; *Pr*, lower molars; *Po*, lower canines.

branched off at an early date from the reptile-root. It follows further with the same absolute certainty that the human race is also a branch of this stem. Man shares all the characteristics I have described with all the Mammals, and differs in them from all other animals. Finally, from these facts we deduce with the same confidence the advances in the vertebrate organization by which one branch of the Saucomammia was converted into the stem-form of the Mammals. Of these advances the chief were: (1) The characteristic modification of the skull

stages in our human genealogy, were first distinguished in 1816 by the eminent French naturalist, Blanville, and received the names of *Oligotrichia*, *Hediphiia*, and *Mesotrichia*, according to the construction of the female organs (oligotrichia = uterus or womb). Husley afterwards gave them the names of *Pseudatheria*, *Metatheria*, and *Aetheria*. But the three sub-classes differ so widely from each other, not only in the construction of the sexual organs, but in many other respects also, that we may confidently draw up the following

Important phylogenetic thesis: The *Mesosaurus*, or *Pseudosaurus* derived from the *Diplocaulus* or *Mesoprosopus*; and the latter, in turn, are descended from the *Mesostoma* or *Oreithiodipus*.

Thus we must regard as the twenty-first stage in our genealogical tree the earliest and lowest chief group of the Mesosaurs—the sub-class of the *Mesostomata* ("classical animals," *Oreithiodipodidae*, or *Pseudosauridae*, Fig. 262 and 263). They take their name from the class which they share with all the lower *Vertebrates*. This class is the common outlet for the passage of the excretaries, the urines, and the sexual products. The urinary ducts and sexual canals open into the bivalve part of the gut, while in all the other Mesosaurs they are separated from the rectum and urea. The latter have a typical *uro-gastric* (urine-gut) arrangement. The bladder also opens into the lumen in the *Mesostomata*, and, indeed, apart from the two *Urotrygonidae*; in all the other Mesosaurs the *Uroteropan* directly into the bladder. It was proved by Huxley and Gauthier in 1881 that the *Mesostomata* lay large eggs like the reptiles, while all the other Mesosaurs are viviparous. In 1882 Richard Owen further proved that these large eggs, rich in yolk-yolk, have a partial yolk-sac and second generation, as I had hypothetically assumed in 1870. Since again they resemble their reptile ancestors. The construction of the mammary gland in the *proboscidea* is the *Mesostomata*. In them the glands have no tube for the young animal to suck, but there is a special part of the breast covered with skin. Not a skin, from which the milk flows, and the young *Mesostomata* drink it all. Further, the brain of the *Mesostomata* is very little advanced. It is smaller than that of any of the other Mesosaurs. The forebrain or cerebrum, in particular, is so small that it does not cover the cerebellum. In the *proboscidea* (Fig. 262) the forebrain of the neocortex among other parts is convex; it is quite different from that of the other Mesosaurs, and rather agrees with that of the reptiles and Amphisbaenidae. Like them, the *Mesostomata* have a strongly developed cerebellum. From these and other less prominent characteristics it follows absolutely that the *Mesostomata* occupy the lowest place among the Mesosaurs, and represent a transition group between the *Therapsida* and the

rest of the Mesosaurs. All these remarkable cephalic characters must have been possessed by the stem-form of the whole advanced class, the *Pseudosauridae* of the Triassic period, and have been inherited through the *Pseudosauridae*.

During the Triassic and Jurassic periods the sub-class of the *Mesostomata* was represented by a number of different stem-ancestors. Numerous fossil remains of them have lately been discovered in the Mesozoic strata of Europe, Africa, and America. To-day there are only two surviving species of the group, which are placed together in the family of the *Oreithiodipodidae*. They are confined to Australia and the neighbouring island of Van Diemen's Land (or Tasmania); they become scarce every year, and will soon, like their *Mesosaurus* relatives, be extinct among the oldest animals. One form lives in the rivers,



Fig. 262.—Skull of a Pseudosauridae (Pseudosaurus) from the Lower Cretaceous of Tasmania. Length, 5 inches. (After Owen.)

and builds subterranean dwellings on the banks; the is the *Oreithiodipodidae*, with webbed feet, a thick soft fur, and broad flat jaws, which look very much like the bill of a duck (Fig. 264, 265). The other form, the land *dipodomys*, or spiny ant-eater (*Oedipodus dipodomys*), is very much like the anterior in its habits and the peculiar construction of its thin nose and very long tongue; it is covered with scales, and can roll itself up like a lightning. A unique form (*Pseudosaurus elegans*) has lately been found in New Guinea.

These curious *Oreithiodipodidae* are the scattered survivors of the vast Mesozoic group of *Mesostomata*; hence they keep the same interest in connection with the stem-form of the Mesosaurs as the living tree-cepsids (*Heterodontidae*) for that of the reptiles, and the isolated *Acanthocephala* for the phylogeny of the *Vertebrates* at all.

The *Acanthocephala* divide themselves into two groups distinguished externally by a certain vir-

like beak or snout. This absence of real body teeth is a late result of adaptation, as in the toothless Placentalia (Sirenia, armadillo and ant-eaters). The extinct Monotremes, to which the Platypus belongs, must have had developed teeth, inherited from the reptiles. Living adult rudiments of real molars have been discovered in the young of the Ostrich-



FIG. 190.—The Ornithorhynchus or Platypus (*Ornithorhynchus anatinus*).

rheus, which has horny plates in the jaws instead of real teeth.

The living Ornithorhynchus and the stem-forms of the Marsupials (or Didelphidae) must be regarded as two widely diverging lines from the Proto-mammals. This second sub-class of the Mammalia is very interesting at a perfect intermediate stage between the other two. While the

Marsupials retain a great part of the characteristics of the Monotremes, they



FIG. 191.—SKELETON OF THE PLATYPUS.

have also acquired some of the chief features of the Placentalia. Some features

are also peculiar to the Marsupials, such as the construction of the male and female sexual organs and the form of the lower jaw. The Marsupials are distinguished by a peculiar hook-like bony process that hangs from the corner of the lower jaw and points forwards. As most of the Placentalia have not this process, we can, with some probability, recognise the Marsupial from its feature alone. Most of the mammal remains that we have from the Jurassic and Cretaceous deposits are merely lower jaws, and most of the jaws found in the Jurassic deposits at Stonesfield and Purbeck have the peculiar bony-lime process that characterises the lower jaw of the Marsupial. On the strength of this palaeontological fact, we may suppose that they belonged to Marsupial Placentalia, or we may suppose that they belonged to Marsupials until towards the close (in the Cretaceous period). At all events, we have no fossil remains of Individually Placentalia from that period.

The existing Marsupials, of which the gliding-hopping kangaroos and the carnivorous opossum (Fig. 270) are the best known, differ a good deal in numbers, shape, and size, and correspond in many respects to the various orders of Placentalia. Most of them live in Australia, and a small part of the Australian and East Malayan islands. There is not a single living Marsupial on the mainland of Europe, Asia, or Africa. It was very different during the Mesozoic and even during the Cretaceous age. The Palaeozoic deposits of those periods contain a great number and variety of marsupial remains, sometimes of a coloured stone, in various parts of the world, and even in Europe. We may infer from this that the existing Marsupials are the survivors of an extensive earlier group that was distributed all over the earth. It had to give way in the struggle for life to the more powerful Placentalia during the Tertiary period. The survivors of the group were able to keep alive in Australia and South America because the two were completely separated from the other parts of the earth during the whole of the Tertiary period, and the other during the greater part of it.

From the comparative anatomy and embryology of the existing Marsupials we may draw very interesting conclusions as to their intermediate position between

the earlier Monotremes and the later Placentalia. The defective development of the brain (especially the cerebellum), the possession of unpaired bones, and the simple construction of the skeleton (without any placenta as yet) were inherited by the Marsupials, with many other features, from the Monotremes, and preserved. On the other hand, they have lost the independent bone formation of the scutellid-blade. But we have a more important advance in the disappearance of the clitoris; the rectum and urea are separated by a partition from the uro-genital opening (*anus proctigaster*). Moreover, all the Marsupials have teeth in the mammary glands, at which the newborn animal feeds. The spots pass into the cavity of a pouch or pocket on the ventral side of the mother, and this is supported by a couple of enlarged bones. The young are born in a very imperfect condition, and carried



The embryo of a marsupial (from a drawing by Mr. G. E. Hart, of Oxford University).

by the mother for some time longer in her pouch, until they are fully developed (Fig. 271). In the giant kangaroo, which is as tall as a man, the embryo only develops for a month in the uterus, it then lives in a very imperfect state, and finishes its growth in the mother's pouch (*metrotrope*); it remains in this abortive condition, and at first hangs suspended on to the test of the mammary gland.

From these and other characteristics (especially the peculiar construction of the internal and external sexual organs in male and female) it is clear that we must suppose the whole sub-class of the Marsupials as one stem group, which has been developed from the Prosimians. From one branch of these Marsupials (possibly from more than one) the class-forms of the higher Mammalia, the Placentalia, were afterwards evolved. Of the existing forms of the Marsupials,

which have undergone various changes through adaptation to different environments, the family of the opossum (*Didelphidae* or *Podomys*) seems to be the oldest and nearest to the common stem-form of the whole class. To this family belong the crab-eating opossums of Brazil (Fig. 272) and the opossums of

Lesser, were evolved directly from the opossum. We must not forget, however, that the conversion of the five-toed foot into a prehensile hand is polyphytic. By the same adaptation to climbing trees the habit of encircling their branches with the feet has in many different cases brought about that opposition of the



FIG. 272.—The prehensile Opossum (*Didelphis marsupialis*). The female has three young in the pouch. (From Selenka.)

Virginia, on the embryology of which Selenka has given us a valuable work (cf. Figs. 63-7 and 272-3). These *Didelphidae* climb trees like the apes, grasping the branches with their hand-shaped hand feet. We may conclude from this that the stem-forms of the Primates, which we must regard as the earliest

threes or great toe to the other toes which makes the hand prehensile. We see this in the climbing lizards (chameleons), the birds, and the tree-dwelling mammals of various orders.

Some zoologists have lately advanced the opposite opinion, that the Mammals represent a completely independent sub-

class of the Monotremes, with no direct relation to the Placentalia, and developing independently of them from the Mammalians. But this opinion is untenable if we examine carefully the whole organization of the three sub-classes, and do not lay the chief stress on incidental features and secondary adaptations (such as the

formation of the *rectus-piureum*). It is then clear that the Marsupials—viviparous Mammals without placenta—are a necessary transition from the oviparous Monotremes to the higher Placentalia with placentae. In this sense the Marsupial class certainly contains some of man's ancestors.

## CHAPTER XXIII.

### OUR APE ANCESTORS

The long series of animal forms which we must regard as the ancestors of our race has been confirmed with greater and greater certainty in our palaeontological inquiry, later presented. The great majority of known animals do not fall in the line of our ancestry, and even within the vertebrates only a small number are found to do so. In the most advanced class of the world, the Chordata, there are only a few families that belong directly in our genealogical tree. The most important of these are the apes and their predecessors, the half-apes, and the earliest Placentalia (*Archonta*).

The Placentalia (the called "higher, Archonta, Anthropoidæ, Apes" or *Simians*) are distinguished from the lower mammals, the two just considered, the Monotremes and Marsupials, by a number of striking peculiarities. Man has all these diagnostic features, that is, a very significant fact! We may, on the ground of the most careful comparative-anatomical and ethnographic research, formulate the thesis: "Man is in every respect a true Placental." He has all the characteristics of structure and development that distinguish the Placentalia from the two lower divisions of the mammals, and, indeed, from all other animals. Among these characteristics we must especially notice the more advanced development of the brain. The fore-brain or cerebrum especially is much more developed in them than in the lower animals. The *cerebellum*, which forms a sort of wide bridge connecting the two hemispheres of the cerebrum, is only fully formed in the

Placentalia; it is very rudimentary in the Marsupials and Monotremes. It is true that the lower Placentalia are not far removed from the Marsupials in cerebral development, but within the placental group we can trace an unbroken gradation of progressive development of the brain, rising gradually from the lowest stage up to the elaborate psychic organ of the apes and man. The human soul—a philosophical function of the brain—is really only a more advanced apportion.

The mammary glands of the Placentalia are provided with ducts like those of the Marsupials, but we never find in the Placentalia the pouch in which the latter carry and suckle their young. Nor have they the overcuped bones in the ventral wall at the anterior border of the pelvis, which the Marsupials have in common with the Monotremes, and which are formed by a partial ossification of the tendons of the inner oblique abdominal muscle. There are merely a few insignificant remains of them in some of the Cetaceans. The Placentalia are also generally without the hook-shaped process at the angle of the lower jaw which is found in the Marsupials.

However, the feature that characterizes the Placentalia above all others, and that has given its name to the whole sub-class, is the formation of the placenta. We have already considered the formation and significance of this remarkable embryonic organ when we traced the development of the chorion and the allantois in the human embryo (pp. 165-9). The misery and the albatross, the

curious vesicle that grows out of the hind part of the gut, has essentially the same structure and function in the human embryo as in that of all the other Amniotes (cf. Figs. 104-6). There is a quite secondary difference, on which great stress has wrongly been laid, in the fact that in man and the higher apes the original cavity of the allantois quickly degenerates, and the rudiment of it sticks out as a small projection from the primitive gut. The thin wall of the allantois consists of the same two layers or membranes as the wall of the gut—the gut-gland layer within and the gut-filter



FIG. 104.—Partial invagination of the human embryo during development in the womb. At first [the two layers (parts) of the body] are folded [the inner layer (inner surface)] over [the outer, the external, membrane (outer surface)]—i.e., folded over towards the middle and [which [now] forms the wall of the embryo—i.e., the body of the embryo—but it is still very far from being fully developed]. The surface [now] facing [the outside] is the yolk-sac [the right side is the yolk-sac]. (From Altmann.)

layer without. In the gut-filter layer of the allantois there are large blood-vessels, which serve for the nutrition, and especially the respiration, of the embryo—the umbilical vessels (p. 170). In the reptiles and birds the allantois enlarges into a spacious sac, which encloses the embryo with the amniotic fluid, and does not communicate with the outer fetal membrane (the chorion). This is the case also with the lowest mammals, the so-called Monotremes and most of the Marsupials. It is only in some of the later Marsupials (*Promyopidae*) and all the Placentalia that the allantois develops into the distinctive

and remarkable structure that we call the placenta.

The placenta is formed by the branches of the blood-vessels in the wall of the allantois growing into the hollow extra-embryonic tufts (villi) of the chorion, which run into corresponding depressions in the mucous membrane of the womb. The latter also is richly permeated with blood-vessels, which bring the mother's blood to the embryo. As the partition in the villi between the maternal blood-vessels and those of the fetus is extremely thin, there is a direct exchange of fluid between the two, and this is of the greatest importance in the nutrition of the young mammal. It is true that the maternal vessels do not entirely pass into the fetal vessels, so that the two kinds of blood are simply mixed. But the partition between them is so thin that the nutritive fluid easily transudes through it. By means of this transudation or diffusion the exchange of fluids takes place without difficulty. The larger the embryo is in the placenta, and the longer it remains in the womb, the more necessary it is to have special structures to meet its great consumption of food.

In this respect there is a very conspicuous difference between the lower and higher mammals. In the Marsupials, in which the embryo is only a comparatively short time in the womb and is born in a very immature condition, the vascular arrangements in the yolk-sac and the placenta suffice for its nutrition, as no food there is the Macropodina, bats, and reptiles. But in the Placentalia, where gestation lasts a long time, and the embryo reaches its full development under the protection of its enveloping membranes, there has to be a new mechanism for the direct supply of a large quantity of food, and this is admirably met by the formation of the placenta.

Bundles of the blood-vessels penetrate into the chorion-villi from within, starting from the gut-filter layer of the allantois, and bringing the blood of the fetus through the umbilical vessels (Fig. 107c). On the other hand, a thick network of blood-vessels develops in the mucous membrane that clothes the inner surface of the womb, especially in the region of the depression into which the chorion-villi penetrate (p. 10). This network of capillaries contains maternal blood, brought by the uterine vessels. As the connective tissue between the enlarged capillaries of

the uterus disappears, wide cavities filled with material blood appear, and into these the chorion-rib of the embryo penetrate. The sum of these vessels of both kinds, that are so intimately correlated at this point, together with the connective and enveloping tissue, is the placenta. The placenta consists, therefore, properly speaking, of two different though intimately connected parts—the fetal placenta (Fig. 273 *obv.*) within and the maternal or uterine placenta (*inv.*) without. The latter is made up of the mucous coat of the uterus and six blood-vessels, the former of the naked chorion and the umbilical vessels of the embryo (of Fig. 196).

The manner in which these two kinds of vessels combine in the placenta, and the structure, form, and size of it, differ a good deal in the various Placentalia; so some extent they give us valuable data

as to birth the fetal placenta alone comes away; the clænæ placenta is not torn away with it.

The formation of the placenta is very different in the second and higher section of the Placentalia, the *Dicroidata*. Here again the whole surface of the chorion is thickly covered with the villi in the beginning. But they afterwards disappear from this part of the surface, and grow proportionately thicker on the other part. We thus get a differentiation between the smooth chorion *fœlicinum* (see, Fig. 273, *obv.*) and the thickly-ribbed chorion *fœlicinum fœlicinum*, Fig. 273, *obv.*). The former has only a few small villi, or none at all, the latter is thickly covered with large and well-developed villi; this alone now constituting the placenta. In the great majority of the Dicroidata the placenta has the same shape as in *caeca* (Figs. 197, 200)—namely



Fig. 197.—Wing of a fossil Icarus (*Apteronotus*), from the Museum of Geology. A lateral view from the right, half natural size. *Oblique* view. *L.* body cavity, *C.* cavity of proctodeum, *M.* muscle.



for the natural classification, and therefore the phylogeny, of the whole of this sub-class. On the ground of these differences we divide it into two principal sections: the lower Placentalia or *faecalis*, and the higher Placentalia or *Dicroidata*.

To the *Indecidua* belong three important groups of mammals: the Lemurs (*Primates*), the Ungulates (cows, horses, deer, ruminants, etc.), and the Cetacea (dolphins and whales). In these holodermes the villi are distributed over the whole surface of the chorion (or its greater part), either singly or in groups. They are only loosely connected with the mucous coat of the uterus, so that the whole fetal membrane with its villi can be easily withdrawn from the uterine depressions like a hand from a glove. There is no real coalescence of the two placentæ at any part of the surface of contact. Hence

a thick, circular disk like a cake; so we find in the Insectivores, Chiroptera, Rodents, and Apes. The *metaplaecæna* lies on one side of the chorion. But in the *Saucomyia* (both the Carnivores and the seals, *Pinnipedia*) and in the elephant and several other Dicroidata we find a *metaplaecæna*; in these the rich mass of villi runs like a girdle round the middle of the elliptical chorion, the two poles of it being free from them.

Still more characteristic of the Dicroidata is the peculiar and very intimate connection between the *chorion fœlicinum* and the corresponding part of the mucous coat of the womb, which we must regard as a real coalescence of the two. The villi of the chorion push their branches into the blood-filled tissues of the coat of the uterus, and the vessels of each loop together so intimately that it is no longer possible to separate the fetal

from the maternal placenta; they form henceforth a compact and apparently simple placenta. In consequence of this coalescence, a whole piece of the lining of the womb comes away at birth with the fetal membrane that is interlaced with it. This piece is called the "falling-away" membrane (*decidua*). It is also called the *serous* (spongy) membrane, because:



FIG. 115.—The Human Fetus (Diagram provided by Captain A. Wilson-Barrett).

it is pierced like a sieve or sponge. All the higher Placentalia that have this decidua are classed together as the "Deciduates." The tearing away of the decidua at birth naturally causes the mother to lose a quantity of blood, which does not happen in the Indicetes. The last part of the uterine coat has to be repaired by a new growth after birth in

the Deciduates. (Cf. Fig. 109, 200, pp. 265-70.)

In the various orders of the Deciduates the placenta differs considerably both in outer form and internal structure. The extensive investigations of the last ten years have shown that there is more variation in these respects among the higher mammals than was formerly supposed. The physiological work of this important embryonic organ, the nutrition of the fetus during its long sojourn in the womb, is accomplished in the various groups of the Placentalia by very different and sometimes very elaborate structures. They have hitherto been fully described by Hare and Hinde.

The physiology of the placenta has become more intelligible from the fact that we have found a number of transitional forms of it. Some of the Marsupials (*Didelphidae*) have the beginning of a placenta. In some of the Lorises (*Lemuridae*) a divided placenta with decidua is developed.

While these important results of comparative embryology have been throwing further light on the close blood-relationship of man and the anthropoid apes in the last few years (p. 172), the great advance of paleontology has at the same time been affording us a deeper insight into the stem-linearity of the Placental group. In the several chapters of my *Synthetic Physique of the Periods* I advanced the hypothesis that the Placentalia form a single stem with many branches, which has been derived from an older group of the Marsupials (*Pseudopachysa*). The four great legions of the Placentalia—Rodents, Ungulates, Carnivores, and Primates—are sharply separated to-day by important features of segmentation. But if we consider their extinct ancestors of the Tertiary period, the differences gradually disappear, the deeper we go in the Cenozoic deposits; in short we find that they vanish altogether.

The primitive stem-forms of the Rodents (*Erithyomysidae*), the Ungulates (*Cervidae*, *Artiodactyla*), the Carnivores (*Felidae*), and the Primates (*Lemuridae*) are as closely related at the beginning of the Tertiary period that we might group them together as different families of one order, the Proplacentalia (*Methatheria* or *Prothecatae*).

Hence the great majority of the Placentalia have no direct and close relationship to man, but only the legend of the *Primates*. This is now generally divided into three orders—the half-apes (*Prosimians*), apes (*Siamangs*), and men (*Anthropoids*). The lemurs or half-apes are the stem-group, descending from the older *Archaeoidea* of the Cretaceous period. From them the apes were evolved in the Tertiary period, and man was formed from them towards its close.

The Lemurs (*Primates*) have five living representatives. But they are very sociable, and are the last survivors of a once extensive group. We find many fossil remains of them in the older Tertiary deposits of Europe and North America, in the Eocene and Miocene. We distinguish two sub-orders, the prosimian Lemuroidea and the modern Lemurinae. The earliest and most primitive forms of the Lemuroidea are the Pachitomids (*Hypalemuridae*), they some exist to the earliest Miocene (*Pachitomus*), and have the typical full dentition, with forty-four teeth (12+12). The *Neotomaenids* (*Adapidae*, *Heg 1914*) have only forty teeth, and have lost an inferior so-called jaw (22+22). The dentition is still further reduced in the Lemurinae (*Amphipithecidae*), which usually have only thirty-six teeth (12+12). These living varieties are scattered over the southern part of the Old World. Most of the species live in Madagascar, some in the Sunda Islands, others in the continent of Asia and Africa. They are gregarious and melanistic animals. They live a quiet life, climbing trees, and eating fruit and insects. They are of different kinds. Some are closely related to the *Marmosids* (especially the *opimus*). Others (*Macrotarsius*) are nearer to the *Indriidae*, others again (*Chiropotes*) to the Rodents. Some of the lemurs (*Hapalemuridae*) approach closely to the true apes. The numerous fossil remains of half-apes and apes that have been recently found in the Tertiary deposits justify us in thinking that our ancestors were represented by several different

species during this long period. Some of these were almost as big as men, such as the dental *Lemurungonoides Megaladapis* of Madagascar.

Next to the lemurs come the true apes (*Siamangs*), the twenty-eighth stage in our ancestry. It has been beyond question for some time now that the apes approach man in every respect of all the animals. Just as the lowest apes come close to the lemurs, so the highest come next to man. When we carefully study the comparative anatomy of the apes and man, we can trace a gradual and uninterrupted advance in the organization of the ape up to the purely human figure, and this proposed examination of the "ape-



Fig. 36.—The unknown ape (*Strepsithecus primigenius*).

problem" that has been discussed of late years with such profound interest, we come finally to the important conclusion, first summarized by Huxley in 1863: "Whatever systems of organs we take, the comparison of their modifications in the various apes leads to the same result: that the most striking differences that separate man from the gorilla and chimpanzee are not so great as those that separate the gorilla from the lower apes." Translated into phylogenetic language, this "pittoresque law," formulated in such masterly fashion by Huxley, is quite equivalent to the popular saying "Man is descended from the apes."

In the very first exposition of his proposed natural classification (1736) Linnaeus

placed the anthropoid mammals at the head of the animal kingdom, with three genera : man, the ape, and the sloth. He afterwards called them the "Primates"—the "lords" of the animal world; he then also separated the lesser from the true ape, and rejected the sloth. Later zoologists divided the order of Primates

and Quadrupeds was retained by Cuvier and most of the subsequent zoologists. It seems to be extremely important, but, as a matter of fact, it is totally wrong. This was first shown in 1863 by Huxley, in his famous *Man's Place in Nature*. On the strength of careful comparative-anatomical research he proved that the



FIG. 277.—The Gibbon (Gibbons). (From Strelitz.)

First the Göttingen anatomist, Blumenbach, founded a special order for man, which he called *Bimana* ("two-handed"); in a second order he united the apes and lemurs under the name of *Quadrupedes* ("four-handed"); and a third order was formed of the distantly-related *Chiroptera* (bats, etc.). The separation of the *Bimana*

apes are just as truly "two-handed" as men; or, if we prefer to reverse it, that man is as truly four-handed as the ape. He showed convincingly that the idea of hand and foot had been wrongly defined, and had been improperly based on physiological instead of morphological grounds. The circumstances that we oppose the

though to the other few fingers in our hand, and as one group things, would it be a special distinction of the hand as contrasted to the foot, in which the corresponding groups are placed in opposed in this way to the others. But the apes can grasp with the hand just as well as the foot, and as were regarded as quadrupeds. However, the inability to grasp, that we find in the form of certain men, is a consequence of the habit of clutching it with tight coverings for thousands of years. Many of the here-found human types of men, especially among the negroes, can the hand very firmly in the same way as the hand. As a result of early habit and continued practice, they can grasp with the foot (as climbing trees, for instance) just as well as with the hand. Even autochthonous Indians of our own race can grasp very strongly with the great toe, and hold a spear with it as firmly as with the hand. Hence the physiological distinction between hand and foot can neither be pressed very far, nor has it a scientific basis. We must look to morphological characters.

As a matter of fact, it is possible to show such a sharp morphological distinction—a distinction based on anatomical structures, between the hand and foot, however. In the human form of the lower extremity and of the members that are connected with the hand and foot before and behind them are material and essential differences, and they are found both in man and the ape. For instance, the number and arrangement of the smaller bones of the hand and foot are quite different. There are other similar differences in the wrists. The hand certainly always has three metacarpal short finger bones; a short ulnar bone, and a long metacarpal; that are not found in the fore extremity. The arrangement of the muscles also is different before and behind. These characteristic differences between the hand and foot extremitiee are found in man as well as the ape. There can be no doubt, therefore, that the ape's hand certainly has more joint articulation at the forearm, first arm, and that all true apes are just as "quadrupeds" as man. The common distinction of the apes as "quadrupeds" is altogether wrong morphologically.

But it may be asked whether, quite apart from this, we can find any other features that distinguish man more sharply from the ape than the number

of species of apes are distinguished from each other. Maudy gives an incomplete and disconnected reply to this question, that the opposable and nonopposable digits to characterize without foundation. On the ground of careful comparative-anatomical research, Huxley proved that in all anthropologists respects the differences between the African and human types are greater than the corresponding differences between the higher apes and man. He thus restored Leidy's order of the Primates (excluding the bats), and divided it into three sub-orders, the first composed of the half-apes (*Lemuridae*), the second of the true apes (*Simiidae*), the third of man (*Hominidae*).

But, as we wish to present this not only briefly and incompletely as the spirit of systematic logic, so may, as the strength of Huxley's case lies, give a good deal further in this division. We are justified in going at least one important step further, and designating one of his natural groups under one of the sub-orders of the order of apes. All the features that characterize this group of apes are found in man, and not found in the other apes. We do not seem to be justified, therefore, in dividing for man a special order distinct from the apes.

The order of the true apes (*Simiidae* or *Pitheciidae*)—excluding the lemurs—has long been divided into two principal groups, which also differ in their geographical distribution. One group (*Pitheciidae*, or "new world") live in America. The other group, to which man belongs are the Anthropidae or "old world" apes; they are found in Asia and Africa, and were formerly in Europe. All the members of this group are the features that are clearly used in morphological classification to distinguish between the two former groups, especially in the dentition. The objection might be raised that the teeth are too subordinate to organic physiologically for us to lay stress on them in suggesting a division. But there is a good reason for it; it is with perfect justice that Huxley's have far more than a merely great particular attention to the teeth in the systematic division and arrangement of the order of mammals. The number, form, and arrangement of the teeth are much more definitely indicated in the various orders than most other characters.

Hence the basis of division is now to say important. In the fully developed

condition we have thirty-two teeth; of these eight are incisors, four canines, and twenty molars. The eight incisors, in the middle of the jaws, have certain

Next to these, at each side of both jaws, is a canine (or "eye tooth"), which is larger than the incisors. Sometimes it is very prominent in man, as it is in most



characteristic differences above and below. In the upper jaw the upper incisors are larger than the others; in the lower jaw the lower are the smaller.

upper and many of the other mammals, and form a sort of tail. Next to this there are five molars above and below on each side, the first two of which (the

"progenitor") we must have only one, and are relegated to the changes of time; the theory back now is that there was one man, and only one, in the original world. The apes of the Old World, or all the living or fossil apes of Asia, Africa, and Europe, form the same division as man.

On the other hand, all the American apes have an additional pro-nasal in each half of the nose. They have also nostrils above and below on each side, or Olfactory nasal slugs. This anatomical difference between the eastern and western apes has been so thoroughly observed that it is very instructive for us. It is true that there seems to be no exception in the case of a small lemur of South America's apes. The small apelike apes (*Australopithecus* or *Proconsul*), which include the *taeniolatus* (*Proconsul*) and the *leucogenys* (*Proconsul*), have only the nostril in each half of the nose (instead of two), and as soon as we come to the eastern apes. But it is found, on closer examination, that they have three nostrils, like all the western apes, and that only the last nose has been lost. Hence the supposed exception really confirms the other distinction.

Of the other features in which the two groups of apes differ, the structure of the nose is particularly massive and complicated. All the eastern apes have the same type of nose as when in comparatively narrow purplish bars up the two halves, so that the nostrils run downwards. In some of them the nose protrudes as far as its nose, and has the same characteristic structure. We have already referred to the curious bengalensis, which have a long, deeply-curved nose. Most of the western apes have, it is true, rather flat noses, like, for instance, the chimpanzee member (Fig. 19); but the nasal partition is thin and narrow in them all. The American apes have a different type of nose. The partition is very broad and thick at the bottom, and the wings of the nostrils are not developed, so that they point backwards instead of downwards. This difference in the form of the nose is so constantly observed in both groups that the apes of the New World are called "the-nosed" (*Platyrrhini*), and those of the Old World "un-nosed" (*Catarrhini*). The long passage of the nose in the bottom of which is the *hypopharynx* is short and wide in all the *Platyrrhini*,

but long and narrow in all the *Catarrhini*; and to cover this difference there is a difference.

This division of the apes into *Platyrrhini* and *Catarrhini*, in the group of the above boundary features, is not generally admitted by zoologists, and receives strong support from the geographical distribution of the two groups in the east and west. It follows at once, as regards the phylogeny of the apes, that two divergent lines presented from the common ancestor of the apes in the early Tertiary period, one of which spread over the Old, the other over the New, World. It is certain that all the *Platyrrhini* arose of one stock, and also all the *Catarrhini*; but the former are phylogenetically older, and hence, be regarded as the stock-group of the lesser.

What can we deduce from this with regard to our own phylogeny? Man had just the same characters, the same form of dentition, auditory passage, and nose as all the *Catarrhini*; in this he really differs from the *Platyrrhini*. We are thus forced to derive him a position among the eastern apes in the order of Primates, or at least place him alongside of them. But it appears that man is a direct blood relative of the apes of the Old World, and can be traced to a common commoner origin with all the *Catarrhini*. In his early organization and in his origin man is a true *Catarrhini*, as organized in the Old World from an unknown earlier group of the eastern apes. The apes of the New World, or the *Platyrrhini*, form a divergent branch of our phylogenetic tree, and this is only directly related to the root of the human race. We need assume, of course, that the eastern African apes had the full division of the *Platyrrhini*. Hence we may regard this stock-group as a sporadic stage (the bengalensis) in our ancestry, and deduce from it for the twenty-eighth stage (the eastern *Catarrhini*).

We have now reduced the state of our present knowledge to the small and comparatively crude group that is represented by the sub-order of the *Catarrhini*, and we are in a position to review the question of man's place in this sub-order, and say whether we add nothing further from this position as to our probable ancestry. In reviewing the question the morphological and paleontological studies that Stanley gives of

the various forms of man, and the various Countries in the Americas are of great assistance to us. It is quite clear from these that the Indians learned man and the Negroid Caucasians (guarani, chiquitanos, and campesinos) are in every respect lighter than the corresponding differences between the Indian and the lower Caucasians (black-skinned savages, negroes, Indians, etc.). In fact, within the small group of the half-breeds not hybridizing, the Indians between the various groups are not less than the differences between them and Negroes. This is seen by a glance at the photographs that Stanley has put together (Fig. 270, etc.). Whether we take the dark or the variegated colour of the hair or the hair in hand tests, or whatever we regard the comparative as the Indians, Negroes, Incas, Pueblos, etc., we always reach the same result as reported earlier—namely, that man is not more different from the other Caucasians than the extreme limits of them (for instance, the gorilla and baboon) differ from each other. We may now, therefore, complete the Hawaiian line we have already started with the following thesis: "Whatever system of origins we take, a comparison of their modifications in the series of Caucasians always leads to the same conclusion, i.e. the successive differences that separate man from the most advanced Caucasians (among gorilla, chimpanzee) are not so great as those that separate the hair from the lower Caucasians (black-skinned savages, negroes, Indians)."

It's more, therefore, consider the degree of separation from other Caucasians to be fully proved. Whatever further information on the comparative anatomy and especially of the living Caucasians we may add to the future, it cannot possibly detract this conclusion. Accordingly, our Caucasians described must have passed through a long series of different forms before the human type was produced. The chief evidence that showed this "series of men," or the differentiation from the ancient colored Caucasians was the adoption of the coat colour and the consequent greater differentiation of the hair and hand tests, the evolution of metaplastic organs and the organ, the eye, and the further development of the brain and its function, the said racial factors had a great influence in this, as Darwin claimed in his famous book.

With an eye to these phenomena we can distinguish at least four important stages in our racial history, which represent previous periods in the historical process of the making of man. We may take after the Indians the earliest and lower Placopithecines of South America, with Otopithecus included, as the lowest stage of our prehistory; they were developed from the Indians by a parallel modification of the brain, teeth, bone, and figure. From these Eocene man-apes were formed the eastern Caucasians, or eastern apes, with the human division (thereby being added by completion of the upper lengthening of the last division of the tail, and the loss of the pre-urine). These eastern man-apes of the whole Caucasians group were in this clearly mixed with man, and had long tails (the *Cyopithecus*, or tailless apes (Mittermeier, Fig. 270). They lived during the Tertiary period, and are found fossilized in the Miocene. Of the several tested apes perhaps the nearest to them are the orangutans.

If we take these Simopithecines as the twenty-second stage in our ancestry, we may put man to them as the twenty-third, the tail-less anthropoid apes. This is the stage given to the most advanced and modified of the existing Caucasians. They were developed from the other Caucasians by losing the tail and part of the hair, and by a higher development of the brain, which found its expression in the continuous growth of the skull. Of the remaining simians there are only a few genera today, and we have already dealt with them (Chapter XV.)—the gibbons (*Hylobates*, Fig. 262) and orang (*Pongo*, Figs. 263, 264) in South-Eastern Asia and the Archipelago; and the chimpanzee (*Chimpanzee*, Figs. 265, 266) and gorilla (*Gorilla*, Fig. 267) in Equatorial Africa.

The great interest that everythropologists attach to these apes arises in view of over two hundred species recently in a fairly large literature. The main division of these works by reported hominoids of the qualities of affinity is Robert Mearns's little work on "The Anthropoid Apes." Mearns divides the primates under two families: (1) Prosimiae (mole and the non-tailless apes), and (2) Simians (tail apes, Caucasians and Placopithecines). Professor K. L. Reich of Halleberg, has submitted a distinct work in his literature and clearly distinguished work on "The Orang and Chimpanzee of Sumatra."

man. This is a substantial supplement to my *Anthropogeny*, in so far as it gives the chief results of modern research on the early history of man and civilization. But when Klaatsch declares the descent of man from the apes to be "irrational, narrow-minded, and false," in the belief that we are thinking of some living species of apes, we must remind him that no competent scientist has ever held so narrow a view. All of us have seen—in the sense of Lazzani and Darwin—to the original unity (admitted by Klaatsch) of the primate stem. That common descent of all the Primates (man, apes, and lemurs) from one primitive stem-form, from which the most far-reaching conclusions follow for the whole of anthropology and ethnology, is admitted by Klaatsch as by myself

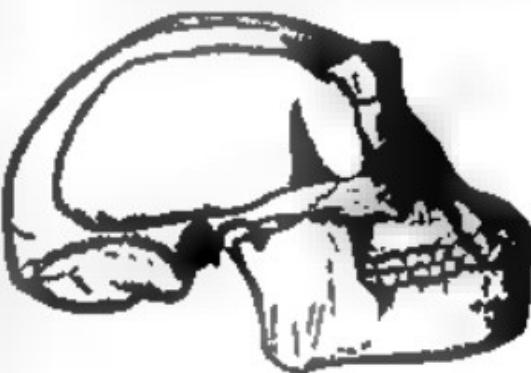
and all other competent zoologists who accept the theory of evolution in general. He says explicitly (p. 172), "The three anthropoid apes—gorilla, chimpanzee, and orang—seem to be branches from a common root, and this was not far from that of the gibbons and man." That is to the main the opinion that I have maintained (especially against Virchow) in a number of works over since 1860. The hypothetical common ancestor of all the Primates, which must have lived in the earliest Tertiary period (more probably in the Cretaceous), was called by me *Avescopus*; Klaatsch now calls it *Proconsul*. Dubois has proposed the specific name of *Prothylopus* to continue and much younger stem-form the anthropomorphs (man and the anthropoid apes).

Drew's

poke. None of these can be said to be absolutely the most man-like. The gorilla comes next to man in the structure of the hand and foot, the chimpanzee in the chief features of the skull, the orang in brain development, and the gibbon in the formation of the chest. None of these existing anthropoid apes is among the direct ancestors of our race; they are scattered survivors of an ancient branch of the Catarrhines, from which the human race developed in a particular direction.

Although man is directly connected with

this anthropoid family and originates from it, we may assign an important intermediate form between the *Prothylopus* and him (the twenty-sixth stage in our ancestry), the australopithecine (*Pithecanthropus*). I gave this name in the *History of Creation* to the "ape-chess primitive man" (*Australopithecus*), which were men in the ordinary sense as far as the general structure is concerned (especially in the differentiation of the teeth), but lacked one of the chief human characteristics, articulate speech and the higher intelligence that goes with it, and so had a less developed brain. The phylogenetic hypothesis of the organization of this "ape-man" which I then advanced was brilliantly confirmed twenty-four years afterwards by the famous discovery of the fossil skull



The skull of the fossil specimen of Java (*Pithecanthropus*), exhibited by Dr. Dubois.

*australopithecus* erected by Eugen Dubois (then military surgeon in Java, afterwards professor at Amsterdam). In 1891 he found at Trinil, in the residency of Madura in Java, in Pliocene deposits, certain remains of a large and very man-like ape (root of the skull, femur, and teeth), which he described as "an exact specimen" and a survivor of a "stem-form of man" (Fig. 281). Naturally, the *Pithecanthropus* excited the liveliest interest, as the long-sought transitional form between man and the ape: we seemed to have found "the missing link." These were very interesting scientific discussions of it at the last three International Congresses of Zoology (Leyden, 1893; Cambridge, 1895, and Berlin, 1901). I took an active part in the discussion at

Cambridge, and may refer the reader to the paper I read there on "The Present Status of Our Knowledge of the Origin of Man" (translated by Dr. Götzen) with the title of *The Last Link*.

An extensive and valuable summary has grown up in the last two years in the *Pithecanthropus* and the *pithecanthropine* theory, associated with it. A number of other pithecanthropines, ammonites, plesiosaurines, and plesiomorphs have a little part in the controversy, and make up of the important data furnished by the new science of prehistoric man. Dr. Maxima Klaatsch has given a good summary of them, with many fine illustrations, in the above-referenced work. I refer the reader to it as a valuable supplement to the present work, especially as I cannot go any further than this anthropological and such-like questions. I will only repeat that I think he is wrong in the attitude of basing, that he efforts to take up with regard to my own view, at the moment of view from the spot.

The most powerful opponent of the Pithecanthropine and the theory of evolution in general—during the last thirty years (until his death in September, 1906)—was the famous Berlin anatomist, Rudolf Virchow. In the speeches which he delivered every year at various conferences and meetings, on the question, he was never tired of attacking the broad "ape theory." His critics' language and phrasing was: "It is quite certain that man does not descend from the ape or any other animal." This has been repeated incessantly by opponents of the theory, especially theologians and physiologists. In the meeting of scientists held in Florence in 1895 at the Anthropological Congress of Venice, he said that "one might just as well have descended from a sheep or an elephant as from an ape." Almost expression like this only shows that the famous pathologist, anatomist, who did so much for medicine in the establishment of cellular pathology, had not the requisite knowledge in comparative anatomy and embryology, systematic biology and paleontology, to understand fully the principles of evolutionary theory. The Rosenberg movement, Götzen-Rosenberg, deserved great praise for giving the moral courage to oppose this dogmatic and exaggerated teaching of Virchow, and showing its absurdity. The recent admirable work of Tiedemann on the *Pithecanthropus*, the author more

of man, and the *Homoanthropus* itself (described) will supply any sound and judicious reader with the empirical material with which he can complete himself of the knowledge of the various degrees of *Vorläufer* and *Urothemen* friends (J. Neander, J. Bechsteiner, etc.).

At the *Pithecanthropus* walked erect, and his brain developed from the capacity of his mother. Fig. 1591 was probably between the human man and the orang-utan age, we must assume that the next great step in the advance from the *Pithecanthropus* to man was the further development of human speech and reason.

Comparative physiology has surely shown that human speech is polyglot in origin; that we must distinguish several (probably many) different primitive tongues that were developed independently. The analysis of language also teaches us that from its beginning, in the child and the primitive, in the most stage human speech first of all gradually developed after the rest of the body had attained its characteristic form. It is probable that language was not much used after the dispersion of the various species and races of men, and this probably took place at the commencement of the Quaternary or Diluvium period. The epoch-historical epoch of Africa certainly reached far into the tail of the Tertiary period, during the Pliocene, probably in the Miocene, period.

The third and last stage of our cultural history is the idea of spirituality (of Homo), who was gradually created from the primitive stage by the advance of civilized language into articulate human speech. As to the time and place of this real "creation of man" we see only certain empirical reasons. It was probably during the diluvial period in the higher zone of the Old World, either in the mainland in Central Africa or Asia, or on an earlier continent (Lemuria)—now sunk below the waves of the Indian Ocean—which stretched from East Africa (Madagascar, Ceylon) to East Asia (China, Japan). Further India. I have given fully in my *History of Culture* (1895, 2nd ed.) the weighty reasons for claiming the descent of man from the *Homoanthropus* tree, and where here we may especially the spread of the human race from the "Promised" over the whole earth. I have also dealt fully with the relations of the various races and species of man to each other.

## SYNOPSIS OF THE CHIEF SECTIONS OF OUR STEM-HISTORY

### First stage : The Prokton.

Man's ancestors are unicellular protists, originally unicellular Monera like the Chromatina, structureless green patches of plasm; afterwards real nucleated cells (first planctonous Proktonytes, like the Radiolaria, then planktogenous Prokton, like the Amoebae).

### Second stage : The Rhizostoma.

Man's ancestors are round colonies or colonies of Proktonytes, they consist of a close association of many heteroprotistal cells, and thus are individuals of the second order. They resemble the round cell-communities of the Radiolarians and Volvox, equivalent to the unicellular blastulae, hollow globules, the wall of which consists of a single layer of situated cells (blastoderm).

### Third stage : The Gastrozoa.

Man's ancestors are Gastrozoa like the simplest of the actual Metazoa (Protoplasm, Olymnia, Hydra, Trichoplacida). Their body consists mainly of a primitive gut, the wall of which is made up of the two primary germinal layers.

### Fourth stage : The Pluteus.

Man's Ancestors have substantially the organization of simple Pluteus (at first like the cryptocoelic Pluteus, later like the rhabdocoelic Turbellaria). The radially-symmetrical body has only one opening, and develops the first trace of a nervous centre from the mid-dorsum in the middle line of the back (Fig. 23, 24).

### Fifth stage : The Tardigrada.

Man's ancestors have substantially the organization of unsarcinated Vermes, at first Gastrotricha (leptidea), afterwards *Bentonia* (*Nemertina*, *Enteropneusta*). Four secondary germinal layers develop, two middle layers moving between the limiting layers (endoderm). The dorsal extension forms the ventral plate, acropagus (Fig. 24).

### Sixth stage : The Proterobranchia.

Man's ancestors have substantially the organization of a simple unsarcinated Chordata (Cephalas and Ascidiaceans). The unsarcinated chords develop between the

dorsal notochordal axis and the ventral gut-tube. The simple coelom-pouches divide by a frontal septum into two on each side; the dorsal pouch (dorsocoel) forms a rhombophore; the ventral pouch (hypocoel) forms a ground. Head-gut with gill-slits.

### Seventh stage : The Annelida.

Man's ancestors are segmented Vertebrates, like the Annelids. The body is a series of metameres, an anterior of the protracting segment, are developed. The head contains in the ventral half the buccal gut, the trunk the hepatic gut. The mid-dorsal tube is still simple. No adult jaws, or teeth.

### Eighth stage : The Crustacea.

Man's ancestors are jawless Crustacea (like the Myriapoda and Pterygotomata). The number of metameres increases. The fore-end of the mid-dorsal tube expands into a head and bears the brain, which soon divides into the cerebral vesicles. In the sides of it appear the three higher sense-organs, ear, eye, and auditory vesicle. No jaws, teeth, or biting mandible.

### Ninth stage : The Insecta.

Man's ancestors are tubular Crustacea: (1) Primitiae fishes (Selachii); (2) plated fishes (Osteocisti); (3) amphibia (Ranidae); (4) shelled amphibia (Stegopoda); The ancestors of this series develop two pairs of limbs, a pair of fore (prothorax) and of hind (metathorax) legs. The gall-bladder are formed between the gall-bladder: the first pair form the muscular Arches (operculum or jetta). The bending muscles (head) and pouches grow out of the gut.

### Tenth stage : The Apeidyle.

Man's ancestors are Amniotes or yolk-less Vertebrates: (1) Primitive Amniotes (Proterozoa); (2) Sauromammals; (3) Primitive Mammals (Monotremes); (4) Marsupials; (5) Lemurs (Primates); (6) Western apes (Pithecines); (7) Eastern apes (Catachines); at first tailless Cynopithecus, then tailless anthropoids; later speechless apes-men (Aka); finally speaking man. The ancestors of these Amniotes develop an amnion and allantois, and gradually assume the mammal, and finally the specifically human, form.

## CHAPTER XXIV.

## EVOLUTION OF THE NERVOUS SYSTEM

The previous chapters have taught us how the human body as a whole developed from the first simple maliment, a single layer of cells. The whole human race owes its origin, like the individual man, to a single cell. The unicellular stem-form of the race is represented daily in the unicellular embryonic stage of the individual. We have now to consider in detail the evolution of the various parts that make up the human frame. I must, naturally, confine myself to the most general and principal features, to make a special study of the evolution of each organ and tissue is both beyond the scope of this work, and probably beyond the scientific capacity of most of my readers to appreciate. In tracing the evolution of the various organs we shall follow the method that has hitherto guided us, except that we shall now have to consider the ontogeny and phylogeny of the organs together. We have seen, in studying the evolution of the body as a whole, that phylogeny casts a light over the darker paths of ontogeny; and that we should be almost unable to find our way in it without the aid of the former. We shall have the same experience in the study of the organs in detail, and I shall be compelled to give simultaneously their ontogenetic and phylogenetic origin. The more we go into the details of organic development, and the more closely we follow the rise of the various parts, the more we see the inseparable connection of embryology and stem-history. The ontogeny of the organs can only be understood in the light of their phylogeny, just as we found of the embryology of the whole body. Each embryonic form is determined by a corresponding stem-form. This is true of details as well as of the whole.

We will consider first the animal and then the vegetal systems of organs of the body. The first group consists of the psychic and the motor apparatus. To the former belong the skin, the nervous system, and the nerve-organs. The motor apparatus is composed of the

passive and the active organs of movement (the skeleton and the muscles). The second or vegetal group consists of the nutritive and the reproductive apparatus. To the nutritive apparatus belong the alimentary canal with all its appendages, the vascular system, and the renal (kidney) system. The reproductive apparatus comprises the different organs of sex (embryonic glands, sexual ducts, and copulatory organs).

As we know from previous chapters (III.-XII.), the animal systems of organs (the organs of nutrition and propagation) develop for the most part out of the outer primary germ-layer, or the cutaneous (skin) layer. On the other hand, the vegetal systems of organs arise for the most part from the inner primary germ-layer, the intestinal layer. It is true that the anthers of the animal and vegetal spheres of the body in man and all the higher animals are by no means rigid; several parts of the animal apparatus (for instance, the greater part of the muscles) are formed from cells that come originally from the endoderm; and a great part of the vegetal apparatus (for instance, the mouth-cavity and the gonoducts) are composed of cells that come from the ectoderm.

In the more advanced animal body there is so much interlacing and interconnection of the various parts that it is often very difficult to indicate the source of them. But, broadly speaking, we may take it as a positive and important fact that in man and the higher animals the chief part of the animal organs comes from the ectoderm, and the greater part of the vegetal organs from the endoderm. It was for this reason that Carl Ernst von Baer called the one the animal and the other the vegetative layer (see p. 164).

The most fundamental of this important class is the gastrula, the most instructive embryonic form in the animal world, which we still find in the same shape in the most diverse classes of animals. This form gives descriptively to a

common stem-form of all the Metazoa, the Gastraea; in this long-antennate organism the whole body consisted throughout like of the two primary germinal layers, as is now the case temporarily in the gastrula; in the Gastraea the simple cutaneous (skin) layer actually represented all the animal organs and functions, and the simple visceral (gas) layer all the vegetal organs and functions. This is the case with the modern Gastraeidae (Fig. 233); and it is also the *a posteriori* with the

We shall easily see that the gastral theory is thus able to throw a good deal of light, both morphologically and physiologically, on some of the chief features of embryonic development. If we take up first the consideration of the chief element in the animal sphere, the psychic apparatus or sensorium and its evolution. This apparatus consists of two very different parts, which seem at first to have very little connection with each other—the outer skin, with all its hairs,

system. This latter comprises the central nervous system (brain and spinal cord), the peripheral, cerebral, and spinal nerves, and the sense-organs. In the fully-formed vertebrate body these two chief elements of the sensorium lie far apart, the skin being external to, and the central nervous system in the very centre of, the body. The one is only connected with the other by a section of the peripheral nervous system and the sense-organs. Nevertheless, as we know from human embryology, the medullary tube is formed from the cutaneous layer. The organs that discharge the most advanced functions of the animal body—the organs of the soul, or of psychic life—develop from the external skin. This is a perfectly natural and necessary process. If we reflect on the historical evolution of the psychic and sensory functions, we are forced to conclude that the cells which accomplish them must originally have been local.

Only elementary organs in this superficial position could directly receive the influences of the environment. Afterwards, under the influence of natural selection, the cellular group in the skin which was specifically "sensitive" withdrew into the inner and more protected part of the body, and formed there the foundation of a central nervous organ. As a result of increased differentiation,

the skin and the central nervous system became further and further separated, —1 in the end the two were only permanently connected by the efferent peripheral sensory nerves.

The observations of the comparative anatomist are in complete accord with this view. He tells us that large numbers of the lower animals have no nervous system, though they exercise the functions of sensation and will like the higher animals. In the unicellular Protozoa, which do not form germinal layers, —1 of course, neither nervous system nor



FIG. 233.—The larva of a Gastraea. Magnified. It shows the epidermis, a layer of mesoglea, a layer of meso-ectoderm of sense-organs, and a layer of ecto-ectoderm (gas). It is a planula larva, but it has not yet developed a mouth or nervous system.

skin. But in the second division of the animal kingdom also, the Metazoa, there is at first no nervous system. Its functions are represented by the simple

lower Metazoa have inherited from the Gastraea (Fig. 233'). We find this in the lowest Zoophytes—the Gastraeidae, Phycosoma, and Sponges (Fig. 233-235). The lowest Cnidaria (the hydrozoan polyp) also are little superior to the Gastraeidae in structure. Their vegetative functions are accomplished by the simple visceral layer, and their animal functions by the simple cutaneous layer. In these

cases the simple cell-layer of the ectoderm is at once skin, locomotive apparatus, and nervous system.

When we come to the higher Metazoa, in which the sensory functions and their organs are more advanced, we find a division of labour among the ectodermal cells. Groups of sensitive nerve cells separate from the ordinary epidermal cells; they retain a protective

the mesoderm;

form special neural groups there. Even in the Platyhelminthes, especially the Trematodes we find an independent nervous system

This is the "upper pharyngeal ganglion," or *acromyophore*, situated above the gut (Fig. 241 A). From this rudimentary structure has been developed the elaborate central nervous system of the higher

In some of

the earth-worms, the first rudiment of the central nervous system



FIG. 242.—Hypodermis of a human embryo at ten months. (From Waldeyer.)

(Fig. 242 A) is a local thickening of the skin-layer (*hs*), which afterwards separates altogether from the horny plate. In the earliest Molluscs (*Cryptoceraspis*) and Vermiforms (*Gasterosteidae*) the accretions form remains in the epidermis. But the medullary tube of the Vertebrates originates in the same way. Our embryology has taught us that this first structure of the central nervous system also develops originally from the outer germinal layer.

Let us now examine more closely the evolution of the human skin, with its various appendages, the glands and glands. The external covering has, physiologically, a double and important part to play. It is, in the first place, the common integument that covers the whole surface of the body, and forms a protective --- layer for the other organs. As such it now effects a certain exchange

between the body and the surrounding atmosphere (respiration, perspiration). In the second place, it is the

1. *protective*  
2. *apparatus*

impermeability of the skin

of isolating the body from (like that of all the higher animals) composed of two layers, skin,

The outer skin, or epidermis, simple ectodermal cells, and contains no blood-vessels (Fig. 242 A, B). It develops

two layers. The underlying skin (skin appendages) consists chiefly of a

numerous general classes of the middle germinative layer, or the desmosome layer. The corium is much thicker than the epidermis. In the deeper strata (the subcutaneum) there are clusters of fibro-cells (Fig. 242 C). The superficial stratum (the cutis proper, or the papillary stratum) forms over almost the whole surface of the body, a number of conical microscopic papillæ (something like *knobs*), which push into the overlying epidermis (c.). These tactile or sensory papillæ contain the fine sensory organs of the skin, the touch corpuscles. Others contain secretory endings of the blood-vessels that nourish the skin (c., d.). The various parts of the corium arise by division of fibres from the originally homogeneous cells of the cutis-plate, the outermost lamina of the mesodermic skin-fibre layer (Fig. 243 A, B, Fig. 2).

In the same way, all the parts and appendages of the epidermis develop by differentiation from the homogeneous cells of this horny plate (Fig. 242 D). At an early stage the simple cellular layer of this horny plate divides into two. The inner and outer stratum (Fig. 242 E) is known as the mucous stratum, the outer and harder (*hs*) as the horny (corneous) stratum. This horny layer is being constantly worn up and rubbed away at the surface; new layers of cells grow up in their place out of the underlying mucous stratum. At first the epidermis is a simple covering of the surface of the body. Afterwards various appendages develop from it, some internally, others externally. The external appendages are the cutaneous glands—sweat, fat, oil,

The external appendages are the hairs and nails.

The cutaneous glands are originally merely solid cone-shaped growths of the epidermis, which sink into the underlying corium (Fig. 286 *a*). Afterwards a canal (Fig. 3) is formed inside them, either by

in or by the secretion of fluid.

Some of the glands, e.g., the sudoriferous, do not secrete (Fig. 286). These glands, which assist in perspiration, are very long, and have spiral coils at the end, but they never secrete, so also the two-glands of the

glans give out buds and secrete; thus, for instance, the lacrimal glands of the upper eyelid that secrete tears (Fig. 286), and the sebaceous glands which secrete the fat in the skin and generally open into the hair-follicles. Sudoriferous and sebaceous glands are found only in mammals. But we find lacrimal glands in all the three classes of Amniotes—reptiles, birds, and mammals. They are wanting in the larva of anamniotes.

The mammary glands (Figs. 287 and

They secrete the milk for the feeding of the new-born animal. In some of their unusual cases, these structures are nothing more than large sebaceous glands in the skin. The milk is formed by the liquefaction of the fatty milk-cells where the branching mammary-gland tubes (Fig. 287 *a*), in the same way as the skin-grease or hair-fat, by the solution of fatty cells inside the sebaceous glands. The outlets of the mammary glands enlarge and form milk-like mammary ducts (*b*), these narrow again (*c*), and open in the teats or nipples of the breast by slits to

The first  
gland  
epidermis,  
corium and

tissues (Fig. 288). These gradually multiply,

the lobes. Thus is formed the pre-natal female breast ( *mammae* ), on the top of which rises the test or nipple (*mamilla* ). The latter is only developed later on, when the mammary gland is fully formed, and this ontogenetic phenomenon is truly interesting, because

mammals (the stern-forms of the whole class) have no tails. In them the milk comes out through a flat portion of the ventral skin that is pierced like a sieve. It is still said in the lowest living marsupial, *Placental Monotreme*, of Australia. The young animal licks the udder with its tongue.

In many of the lower mammals we find a number of milk-glands at different parts of the ventral surface. In the human female there is usually only a pair of glands, at the breast; and it is the same with the apes, bats, elephants, and several other mammals. Some

find successive pairs of



The lactiferous mammary gland from a human infant of four months. (From Abderh.) External structure, in the shape of a single oval organ, with several smaller processes, rounded and lobulated, called buds, constituting one of the hollow bodies of alveoli.

glands (or even more).

Female. Some species of breasts, like pigs and hedgehogs (Fig. 289). This polymorphism points back to an older stern-form.

Male

(Fig. 293 *D*). Sometimes, moreover, the external mammary glands are fully developed and can lactate in the male, but

organs without function in the male. We have already (Chapter XI) dealt with this remarkable and interesting instance of viviparity.

While the cutaneous glands are inner growths of the epidermis, the appendages

which we call hairs and spines are external local growths in it. The walls of *Crocodiles*,

which se-

mily

Instead of them; the mammals—  
the stem-form of the mammals  
had claws; we find them in a mammalian  
form even in the marsupial. The horny  
claws are highly developed in most of the  
reptiles (Fig. 264, p. 245), and the mam-  
mals have inherited them from the earliest  
representatives of this class, the syn-  
apsids (*Temnospondyls*). Like the hoof-



FIG. 264.—The Stomach of *Emydocephalus* (a species of monitor lizard). Enlarged 10 times, a narrow tube, which opens into the oesophagus (From H. Müller.)

*insects* / of the Crustacea the walls of  
spines and hairs have been evolved from the  
claws of the older mammals. In the  
human embryo the first rudiment of the  
nails is found (between the horny and the  
meadow stratum of the epidermis) in the  
fourth month. But these edges do not  
penetrate through until the end of the  
sixth month.

The most interesting and important  
appendages of the epidermis are the  
hairs; on account of their peculiar com-  
position and origin we must regard them  
as highly characteristic of the whole  
mammalian class. It is true that we also  
find hairs in many of the lower animals,

birds, like the hairs of plants, are thread-like appendages of the surface, and differ widely from the hairs of the mammals in the details of their structure and develop-

#### physiology of the hair

views as to their phylogeny. On the older view the hairs of the mammals are equivalent or homologous to the feathers of the bird or the horny scales of the reptile. As we deduce all three classes of Amniotes from a common stem-group, we must assume that these Devonian synapsids had a complete hairy coat, inherited from their Carboniferous ancestors, the naked amphibia (*Sarcopterygia*); the bony scales of their epidermis were covered with horny scales. In passing from aquatic to terrestrial life the horny scales were further developed, and the bony scales degenerated in most of the reptiles. As regards the bird's feathers, it is certain that they are modifications of the horny scales of their reptilian ancestors. But it is otherwise with the hairs of the mammals. In their case the

but lately been advanced on  
of very extensive research,  
by Friedrich Maunder, that they

evolved from the cutaneous  
sense-organs of amphibia ancestors by  
modification of functions; the epidermal  
structure is very similar in both to its  
embryonic rudiments. This modern view,  
which had the support of the greatest  
expert on the vertebrates, Carl Gegenbaur,  
can be harmonized with the older theory  
to an extent, in the sense that both  
the scales and hairs, were very  
closely associated originally. Probably  
the budding off the skin-tissue  
in *Amphibia* under the protection of air,  
or

much subsequently by the cornification of  
the hairs; many hairs are still sensory  
organs ( tactile hairs on the muscle and  
tissues of many mammals; pubic hairs).

The middle position of the genetic connection of scales and hairs was advanced in my *Synthetic Phylogeny of the Vertebrates* (p. 433). It is confirmed by the similar arrangement of the two cutaneous formations. As Maunder pointed out, the hairs, as well as the cutaneous  
sense-organs and the scales, are at first arranged in regular longitudinal series,  
and they afterwards break into alternate  
groups. In the embryo of a bear two

inches long, which I owe to the kindness of Herr von Schmetzinger (of Arva Varalia, Hungary), the back is covered with sixteen to twenty alternating longitudinal rows of acutely protuberances (Fig. 115). They are at the same time arranged in regular transverse rows, which converge at an acute angle from both sides towards the middle of the back. The tip of the scale-like warts is turned inwards. Between these larger hard scales (or groups of hairs) we find numbers of rudimentary smaller hairs.

The human embryo is, as a rule, entirely clothed with a thick coat of fine hair.

Ring the last three or four weeks of gestation. This embryonic situation continues generally unchanged in part during the first weeks of fetal life, but in any case, as it follows, it is lost at birth, and is replaced by the thinner coat of the newborn.

This permanent hair, the coat of hair-follicles, which are given off from the epidermis of the skin, may now appear. The embryonic hair-coat is wavy, on the skin of the human embryo, covers the whole body, with the exception of the palms of the hand and soles of the feet.

These hairs are always bare, as in the case of apes and of most other mammals; sometimes the wool-coat of the embryo has a striking effect, in its colour, on the later permanent hair-coat. Hence it happens occasionally, for instance, among our Indo-Germanic races, that children of blond parents seem—so to speak of the latter—to be covered at birth with a dark brown or even a black woolly coat. Not until this has disappeared do we see the permanent blond hair which the child thus inherited. Structures like this last for a week, and even more, after birth. This remarkable woolly coat of the human embryo is a legacy from the apes, our ancient long-haired ancestors.

It is not less noteworthy that many of the higher apes approach man in the thinness of the hair on various parts of the body. With those of the apes, especially the higher Catarrhines (or man-voiced apes), the face is mostly, or entirely, bare, or at least it has hair no longer or thicker than that of man. In these cases, too, the back of the head is usually provided with a thicker growth of hair: this is lacking, however, in the case of the bald-headed chimpanzee (*Chimpanzee calvus*). The males of many species of apes have a considerable beard on the

cheeks and chin; this sign of the masculine sex has been acquired by sexual selection. Many species of apes have a very thin covering of hair on the breast and the upper side of the limbs—thinner than on the back or the under side of the limbs. On the other hand, we are often accustomed to find tufts of hair on the shoulders, back, and extremities of members of our Indo-Germanic and of the Semitic races. Exceptional hair on the face, as on the whole body, is hereditary to certain families of hairy men. The quantity and the quality of the hair on head and chin are also comparatively transmitted in families. The extraordinary variations in the usual or partial hairy coat of the body, which is so noticeable, not only in comparing



The all-mammalian gland of a newborn human embryo (normal head and neck)

different races of men, but also in comparing different families of the same race, can only be explained on the assumption that in man the hairy coat is, on the whole, a rudimentary organ, a useless inheritance from the more thickly-coated apes. In this man resembles the elephant, rhinoceros, hippopotamus, whale, and other mammals of various orders, which have also, almost entirely or for the most part, lost their hairy coats by adaptation.

The particular process of adaptation by which man lost the growth of hair on most parts of his body, and retained as suggested it at some points, was most probably sexual selection. As Darwin ingeniously showed in his *Descent of Man*, sexual selection has been very active

in this respect. As the male anthropoid apes chose the females with the least hair, and the females favoured the males with the finest growths on chin and head, the general covering of the body gradually degenerated, and the hair of the beard and head was more strongly developed. The growth of hair at other parts of the body (acro-pit, pubic region) was also probably due to sexual selection. Moreover, changes of climate, or habits, and other adaptations unknown to us, may

have done—gorilla, chimpanzee, orang, and several species of gibbon—besides man (Figs. 303, 304). In other species of gibbons the hairs are pointed towards the hand both in the upper and lower arm, as in the rest of the mammals. We can easily explain this remarkable peculiarity of the anthropoids and man on the theory that our common ancestors were accustomed (as the anthropoid apes are to-day) to place their hands over their heads, or across a branch above their



FIG. 303.—Variety of a hairy (Gibbons' 303), when raised up—A from the right, B from the left.

have assisted the disappearance of the hairy coat.

The fact that our coat of hair is inherited directly from the anthropoid apes is proved in an interesting way, according to Darwin, by the direction of the rudimentary hairs on our arms, which cannot be explained in any other way. Both on the upper and the lower part of the arm they point towards the elbow. Here they meet at an obtuse angle. This curious arrangement is found only in the anthro-

poids, during court. In this position, the fact that the hairs point downwards helps the rain to run off. Thus the direction of the hair on the lower part of our arm reminds us to-day of that useful custom of our anthropoid ancestors.

The nervous system in man and all the other vertebrates is, when fully formed, an extremely complex apparatus, that we may compare, in anatomical structure and physiological function, with an extensive telegraphic system. The chief stations of

the system is the central marrow or central nervous system, the immovable ganglionic cells or neurons (Fig. 39) of which are connected by branching processes with each other and with numbers of very fine conducting wires. The latter are the peripheral and ubiquitous nerve-fibres; with their terminal apparatus, the sense-organs, etc., they constitute the conducting marrow or peripheral nervous system. Some of them—the sensory nerve-fibres—conduct the impressions from the skin and other sense-organs to the central marrow; others—the motor nerves—convey the commands of the will to the muscles.

The central nervous system or central marrow (*medulla cordis*) is the real organ of psychic action in the nervous series. However we conceive the intimate connection of this organ and its functions,

which we call sensation, we are inextricably dependent development of the two man and all the higher

give us most important information regarding the nature of the "self," it should be full of interest. If the central marrow develops in just the same way in the human embryo as in the embryo of the other mammals, the evolution of the human psychic organ from the central

them from the lower vertebrates, must beyond question. No one can doubt a momentous bearing of these embryonic phenomena.

In order to understand them fully we set first a word or two of the general and the anatomical composition of the human central nervous system (the central nervous system of all the other Craniotes, it consists of two parts, the brain-marrow or brain (*medulla cerebri et encephali*) and the spinal-marrow (*medulla spinalis* or *metacordis*). The one is enclosed in the bony skull, the other in the bony vertebral column. Twelve pairs of cerebral nerves proceed from the brain;

spinal nerves—  
rest of the body (Fig. 371). On a  
natomistic investigation the spinal  
is found to be a cylindrical cord,  
it both in the region  
of the last  
vertebrae) and the region of the lumbæ (at

the first lumbar vertebra) below (Fig. 371). At the cervical half the strong nerves of the upper limbs, and at the lumbar both those of the lower limbs, proceed from the spinal cord. Above, the latter passes into the brain through the medulla oblongata (Fig. 393 and 396). The spinal cord appears to be a thick mass of nervous matter, but it has a narrow canal at its axis, which passes into the further



The eye. The eye.

The eye.

FIG. 393.—Sagittal section of the human embryo at the cervical part, from the dorsal side. Brain and spinal cord exposed. (Clark's Anatomy.) A section of the spinal marrow; blood, or oxygen quadruplex (according to Huxley); under it, medulla oblongata (after Brown).

FIG. 394.—Central nervous system of a human embryo, four months old, viewed from the back. (Clark's Anatomy.) A large cerebrum, a cerebellum, a medulla oblongata, underneath it the spinal cord.

cerebral ventricles above, and is filled, like these, with a clear fluid.

The brain is a large, roughly spherical part of the skull, of elaborate structure. On general examination it divides into two parts, the cerebrum and cerebellum. The cerebrum lies in front and above, and has the familiar characteristic convolutions and furrows on its surface (Figs. 392, 393). In the upper side it is divided by a deep longitudinal fissure into two halves,

lateral hemispheres; these are connected by the *anterior commissum*. The large hemisphere is separated from the small cerebellum by a deep transverse fissure. The latter lies behind and below, and has also numbers of fissures, but much less and more regular, with commissures between, at its surface. The cerebellum is divided by a longitudinal fissure into two halves, the "small hemispheres." These are connected by a *worm-shaped* place, the *anterior commissum*, above, and by the broad *posterior commissum* (Fig. 324, 17).

The sympathetic system and ganglia, such as that in man and all the other

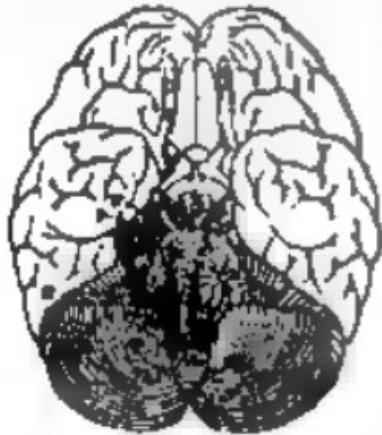


FIG. 324.—The Frog's Brain, seen from below (from A. Agassiz). Above, the brain; below, the spinal cord. The spinal cord is broken across, below (dotted), to give a better view of its interior (ventral) surface. The dotted portion indicates the limits of the smaller process of ventral nerves as it meets beneath the cord.

Cerebrum the brain is at first composed of three parts, but of these, and afterwards five, successive parts. These are found in just the same form—in five consecutive vesicles—in the embryo of all the Craniota, from the Cyclostoma and Fishes to man. But, however much they agree in their rudimentary condition, they differ considerably afterwards. In man and the higher mammals the first of these vesicles, the cerebrum, grows so much that in its mature condition it is by far the largest and heaviest part of the brain. To it belong not only the large hemispheres, but also the corpus callosum that joins them, the olfactory fibers,

from which the olfactory nerves start, and most of the structures that are found at the roof and bottom of the large lateral ventricles outside the two hemispheres, such as the optic chiasm. On the other hand, the optic chiasm, which lies between the lobes, belongs to the second division, which develops from the "intermediate brain," to the same extent, holding the single third cerebral ventricle and the structures that are known as the corpora quadrigemina, the infundibulum, and the pituitary gland. Behind these parts we find, between the cerebrum and cerebellum, a small ganglion composed of two ganglia, which is called the *anterior pituitary-ganglion* on account of a superficial transverse groove cutting across (Fig. 324, 17). Although this quadrigeminal ganglion is very large indeed in man and the higher mammals, it forms a *spared* third ventricle, greatly developed in the lower vertebrates, the "midline nippes." The fourth section is the "hind-brain" or *metencephalon* (cerebellum) to the warmer sides, with the *bulb* median part, the pons, and the pair of lateral parts, the "small hemispheres." (Fig. 324, 17.) Finally, we have the fifth and last section, the medulla oblongata (Fig. 324, 17), which contains the single fourth cerebral ventricle and the caudal (cauda) part (*myelophyllum*, *cauda*, *corpus caudatum*). The medulla oblongata passes straight into the medulla spinalis (spinal cord). The anterior cerebral canal of the spinal cord continues above into the quadrigeminal fourth ventricle of the medulla oblongata, the floor of which is the quadrigeminal depression. This is a narrow duct, called "the aqueduct of Sylvius," passing through the corpus quadrigemina to the third cerebral ventricle, which lies between the two optic thalamoi and this in turn is connected with the pairs of lateral ventricles which lie in the right and left in the large hemispheres. Through the canals of the central nervous system are directly interconnected. All these parts of the brain have an infinitely complex structure in detail, but we cannot picture this. Although it is much more elaborate in man and the higher Vertebrates than in the lower classes, it develops in them all from the same rudimentary structures, the five simple cerebral vesicles of the embryonic brain.

But before we consider the development of the complicated structures of the brain from this simple state of vesicles, let

us glance for a moment at the lower invertebrates, which have no brain. Even in the skull-less vertebrate, the Amphioxus, we find no independent brain, as we have seen. The whole central nervous system is merely a simple cylindrical cord which has the length of the body, and ends equally simply at both extremities—a plain medullary tube. All that we can discover is a small vesicular bulge at the foremost part of the tube, a degenerate rudiment of a primitive brain. We meet the same simple medullary tube in the first structure of the ascidio larva, in the same characteristic position, above the pharynx. On closer examination we find here also a small vesicular swelling at the fore end of the tube, the first trace of a differentiation of it into brain and spinal cord. It is probable that this differentiation was more advanced in the earliest Vertebrates, and the brain-cord more pronounced (Fig. 212). The brain is physiologically older than the spinal cord, as the trunk was not developed until after the head. If we consider the embryological history of the brain to the Vermiform, and remember that we can trace all the Chordons to lower Vermiforms, it seems probable that the simple central nervous system of the former is equivalent to the simple nervous ganglion, which lies above the shield in the lower worms, and has long been known as the "upper pharyngeal ganglion." *Amphioxus* (*Pharyngocoelus*, etc.), it would be better to call it the anterior or ventral brain (*metacerebrum*).

Probably this upper pharyngeal ganglion of the lower worms is the structure from which the complex central nervous system of the higher animals has been evolved. The medullary tube of the Chordons has been formed by the lengthening of the ventral brain on the dorsal side. In all the other animals the central nervous system has been developed in a totally different way from the upper pharyngeal ganglion; in the Articulates, especially, a pharyngeal ring, with ventral marrow, has been added. The Molgulæ also have a pharyngeal ring, but it is not found in the Vertebrates. In them the central

marrow has been prolonged down the dorsal side, in the Articulates down the ventral side. This fact proves of itself that there is no direct relationship between the Vertebrates and the Articulates. The undulatory attempt to draw the dorsal marrow of the former from the ventral marrow of the latter has totally failed (cf. p. 319).

When we examine the embryology of the human nervous system, we must start from the important fact, which we have already seen, that the first structure of it is one and all the higher Vertebrates is the simple medullary tube, and that this separates from the outer germinative layer in the middle line of the so-called



FIG. 212.—The human brain, seen from the left. (From P. Müller.) The forms of the convolutions are indicated by black dots around the circulation of their lines. Under the label are given the following abbreviations: 1, Optic nerve; 2, cerebral cortex; 3, corpus callosum; 4, fornix; 5, hippocampus; 6, parahippocampal gyrus; 7, amygdala; 8, nucleus opticus.

epibolytic shield. As the reader will remember, the straight medullary furrow first appears in the middle of the semihorseshoe-shaped embryonic shield. At each side of it the parallel borders curve over in the form of dorsal or medullary swellings. These bend together with their free borders, and thus form the closed medullary tube (Figs. 133-137). At first this tube lies directly underneath the horny plate; but afterwards it turns towards the upper edge of the prevertebral plate growing together between the horny plate and the tube, joining above the latter, and forming a completely closed canal. As Goettsewe very properly observes, "this growth is hindering in the

inner part of the body is a potence associated with the progressive differentiation and the higher potentiality that this secures; by this process the power of greater value in the organism is "held within the frame" (Cf. Papez, 193-194).

In the Cyclostomes—a stage above the Acanthia—the first end of the cylindrical medullary tube begins early to expand into a pear-shaped vesicle; this is the first outline of an independent brain. In this way the central nervous system of the Vertebrates divides clearly into its two chief sections, brain and spinal cord. The simple vesicular form of the brain, which persists for some time in the Cyclostomes, is found also at first in all the higher Vertebrates (Fig. 153, 163). But in these it soon passes away, the one vesicle being divided into several successive parts by transverse constrictions. There are first two of these constrictions,



Fig. 153.

Fig. 163.

Fig. 164.

Fig. 153-164.—Sagittal sections of the brains of Cyclostomes from the second week to the third month. Fig. 153 shows the first vesicle, brain and spinal cord separate. Fig. 163 shows the first transverse constriction, and Fig. 164 shows the second transverse constriction. (After Papez, 1933, from a photograph of his own drawings.)

dividing the brain into three successive vesicles (fore brain, middle brain, and hind brain, Fig. 153 n, m, n). Then the fore and third are subdivided by brain constrictions, and thus we get the successive sections (Fig. 153).

In all the Craniotes, from the Cyclostomes up to man, the same parts develop from these five original cerebral vesicles, though in very different ways. The first vesicle, the fore brain (Fig. 153 n), forms by far the largest part of the cerebrum—namely, the large hemispheres, the olfactory lobes, the corpora striata, the calcarous, and the fornix. From the second vesicle, the intermediate brain (n), originate especially the hypothalamus, the other parts that surround the third ventricle and infundibulum, and the infundibulum and pituitary gland. The third vesicle, the middle brain (m), produces the deeper optic ganglion and

the aqueduct of Sylvius. From the fourth vesicle, the hind brain (n), develops the greater part of the cerebellum—namely, the corpus and the two small hemispheres. Finally, the fifth vesicle, the after brain (o), forms the medulla oblongata, with the quadrangular pit (the floor of the fourth ventricle), the pyramids, alveolar nucleus, etc.

We must certainly regard it as a comparative-anatomical and ontogenetic fact of the greatest significance that in all the Craniotes, from the lowest Cyclostomes and fishes up to the apes and man, the brain develops in just the same way in the embryo. The first rudiment of it is always a simple vesicular enlargement of the fore end of the medullary tube. In every case, then, there are five vesicles developed from this bulk, and the permanent brain with all its complex anatomic structures, of so great a variety in the various classes of Vertebrates, is formed from the five primative vesicles. When we compare the various brains of a fish, an amphibia, a reptile, a bird, and a mammal, it seems incredible that we can trace the various parts of those organs, that differ so much internally and externally, to common types. Yet all these different Craniotic brains have started with the same Rudimentary BRAIN-TUBE. To continue our study of this we have only to compare the corresponding stages of development of the embryos of these different animals.

The comparison is extremely interesting. If we extend it through the whole series of the Craniotes, we soon discover this interesting fact: In the Cyclostomes (the Myxinoidea and Pteroveneropidae), which we have recognized as the lowest and earliest Craniotes, the whole brain remains throughout life at a very low stage, which is very brief and passing in the embryos of the higher Craniotes: they return the five original sections of the brain unchanged. In the fishes we find an essential and considerable modification of the five vesicles: it is clearly the brain of the Selachii in the first place, and subsequently the brain of the Gadoids, from which the brain of the rest of the fishes or the one broad end of the Diplopoda and Amphibia, and through them of the higher Vertebrates, on the other hand, must be derived. In the fishes and Amphibia (Fig. 160) there is a preponderant development of the middle brain, and also the other brain, the first, second, and

fourth sections remaining very primitive. It is just the reverse in the higher Vertebrates, in which the first and third sections, the cerebrum and cerebellum, are exceptionally developed; while the



Fig. 29.—Head of a chick embryo (aged 14½ hours), seen from above, showing the forebrain, midbrain, hindbrain, and cerebellum. The cerebrum is at its minimum, so that both the forebrain and hindbrain are large, in the form of bulbous lobes, so called then, to protect against the spinal fluid.

middle brain and after brain remain small. The corpora quadrigemina are mostly covered by the cerebrum, and the oblongata by the cerebellum. But we find a number of stages of development within the Higher Vertebrates themselves. From the Amphibia upwards the brain (and with it the psychic life) develops in two different directions; one of them is followed by the reptiles and birds, and the other by the mammals. The development of the first section, the fore brain, is particularly characteristic of the mammals. It is only in them that the cerebrum becomes so large as to cover all the other parts of the brain (Figs. 295, 301-304).

There are also notable variations in the relative position of the cerebral vesicles. In the lower Crustaceans they lie originally almost in the same plane. When we examine the brain laterally, we can cut through all five vesicles with a straight line. But in the Amniotes there is a considerable curve in the brain along with the bending of the head and neck; the whole of the upper dorsal surface of the

brain develops much more than the under ventral surface. This causes a curve, so that the parts come to lie as follows: The fore brain is right in front and below, the intermediate brain a little higher, and the middle brain highest of all; the hind brain lies a little lower, and the after brain lower still. We find this only in the Amniotes—the reptiles, birds, and mammals.

Thus, while the brain of the mammals agrees a good deal in general growth with that of the birds and reptiles, there are some striking differences between the two. In the Sauropsidae (birds and reptiles) the middle brain and the middle part of the hind brain are well developed. In the mammals these parts do not grow, and the fore-brain develops so much that it covers the other vesicles. As it continues to grow towards the rear, it at last covers the whole of the rest of the brain, and also encloses the middle parts from



Fig. 290.—Stages of three crustacean embryos to which A is the earliest, B of a dibrach (Mediterranean), C of a pentadactyl (Capricorn). A, forebrain, B, intermediate brain, C, middle brain, a, forebrain, b, intermediate brain, c, middle brain, d, after brain, e, cerebellum, f, ganglion cells. (From Gegenbaur.)

Fig. 291.—Brain of a shark (Squalus) seen from above. A, forebrain, B, intermediate brain, which need not be the largest; C, middle brain, behind the valvula; D, posterior brain, E, cerebellum, F, after brain. (From Gegenbaur.)

the valve (Figs. 301-304). This process is of great importance, because the fore brain is the organ of the higher psychic life, and in it those functions of the nerve-cells are discharged which we sum up in

the word "zoob." The highest achievements of the animal body—the wonderful manifestations of consciousness and the complex molecular processes of thought—have their seat in the fore-brain. We can remove the large hemispheres, piece by

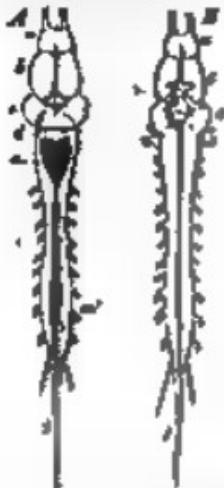


FIG. 20.—Brain and spinal cord of the dog at three months, A, from an animal just twenty days before the (A) were born, i.e., immediately after birth or the intermediate form, a middle form of the adult, and B, a young dog, one year old, i.e., a typical adult. (After H. G. Wells, *in: The Progress of the Dog*, 1902.)



FIG. 20.—Brain of an adult dog, two years old. (From H. G. Wells, *in: The Progress of the Dog*, 1902.) The lateral wall of the left hemisphere has been removed. a, corpora striata; m, olfactory commissure; s, corpus callosum; v, ventricular system; w, roof of the fourth ventricle. At year. Varro, no caption available.

piece, from the mammal without killing it, and we then see how the higher functions of consciousness, thought, will, and sensation, are gradually destroyed, and in the end completely extinguished. If the animal is fed artificially, it may be

kept alive for a long time, as the destruction of the psychic organs by no means involves the extinction of the faculties of digestion, respiration, circulation, urination—in a word, the vegetative functions. It is only conscious sensation, voluntary movement, thought, and the combination of various higher psychic functions that are affected.

The fore-brain, the organ of those functions, only attains this high level of development in the more advanced Placentalia, and thus we have the simple explanation of the intellectual superiority of the higher mammals. The soul of most of the lower Placentalia is not much above that of the reptiles, but among the higher Placentalia we find an uninterrupted gradation of mental power up to the apes and man. In harmony with this we find an astonishing variation in the



FIG. 20.—Brain of a human embryo, tripled in size, of one month, second month, third month, and fourth month. The cerebrum, the cortex, increases rapidly, while the smaller medullary parts, the cerebellum, the pons, the midbrain, the medulla oblongata, increase slowly.

degree of development of their fore-brain not only qualitatively, but also quantitatively. The mass and weight of the brain are much greater in modern mammals, and the differentiation of its various parts more important, than in their earliest Tertiary ancestors. This can be shown paleontologically in any particular order. The brains of the living ungulates are (relatively to the size of the body) four to six times (in the highest groups even eight times) as large as those of their earliest Tertiary ancestors, the well-preserved skulls of which enable us to determine the size and weight of the brain.

In the lower mammals the surface of the cerebral hemispheres is quite smooth and level, as in the rabbit (Fig. 204). Moreover, the fore-brain remains so small that it does not cover the middle brain. At a stage higher the middle

brain is covered, but the hind brain remains free. Finally, in the ape and man, the latter also is covered by the forebrain. We can trace a similar gradual development in the apes and com-

pare them with man. It has been discovered that this is not the case, but that the characteristic features of the human brain are found in a rudimentary form in the lower apes, and are more or less fully developed in the higher apes. Huxley has convincingly shown, in his *Men's Brain vs. Nature* (1868), that the difference in the formation of the brain within the simian group constitutes a deeper gulf between the lower and higher apes than between the higher apes and man.

The comparative anatomy and physiology of the brain of the higher and lower mammals are very instructive, and give important information in connection with the chief questions of physiology.

The central nervous system (brain and spinal cord) develops from the medullary tube in man just as in all the other mammals, and the same applies to the conducting network of "peripheral nervous system." It consists of the sensory nerves, which conduct centripetally the


 Fig. 294.—Brain of a human embryo, represented under old division of the main parts: right hemisphere on the left side of the figure, left hemisphere on the right side. The diagram shows the internal structures of the brain at an early developmental stage.

impulses that are found on the surface of the cerebrum of the higher mammals (Huxley, 1868, 1871). If we compare different groups of mammals in regard to these brains and convolutions, we find that their development proceeds step by step with the advances of mental life.

Of late years great attention has been paid to this special branch of cerebral anatomy, and very striking individual differences have been discovered within the limits of the human race. In all human beings, of special gifts and high intelligence the convolutions and fissures are much more developed than in the average man, and they are more developed in the latter than in apes, and others of low mental capacity. There is a similar gradation among the mammals in the internal structure of the fore brain. In particular the corpus callosum, that unites the two cerebral hemispheres, is only developed in the Placentalia. Other structures—for instance, in the lateral ventricle—that seem at first to be peculiar to man, are also found in the higher apes, and these alone. It was long thought that man had certain distinctive organs in his cerebrum which were not found in any other animal. But careful examina-

tion also in man just as in all the other mammals, and the same applies to the conducting network of "peripheral nervous system." It consists of the sensory nerves, which conduct centripetally the

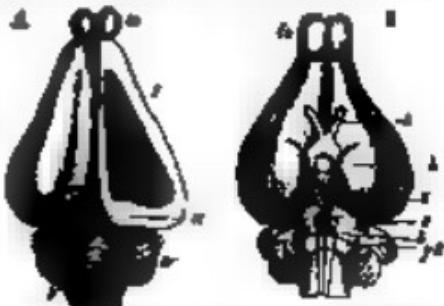


Fig. 295.—Brains of the rhesus. A: From the dorsal; B: from the ventral side. In rhesus below, I, optic nerve; II, hypophysis; III, body of the interpeduncular brain; IIII, midbrain; V, tentorial brain; VI, optic nerve; VII, nucleus nervi facialis; VIII, auditory nerve. In A the roof of the right hemisphere (I) is removed so that we can see the corpora quadrigemina in the lateral ventricle. (From Gegenbaur.)

Impressions from the skin and the sense-organs to the central nervous, and of the motor nerves, which convey centrifugally the movements of the will from the central nervous to the muscles. All these

peripheral nerves grow out of the medullary tube (Fig. 171), and are, like it, products of the skin-sense layer.

The complete agreement in the structure and development of the psychic organs which we find between man and the highest mammals, and which can only be explained by their common origin, is of profound importance in the comparative psychology. This is only seen in full light when we compare these morphological facts with the corresponding physiological phenomena, and remember that every psychic action requires the complete and normal condition of the cerebrative brain structure for its full and normal existence. The very complex muscular movements inside the neural cells, which we describe comprehensively as "the life of the soul," can no more exist in the vertebrates, and therefore in man, without their organs than the circulation

without the heart and blood. And as the central nervous develops in man from the same medullary tube as that of the other vertebrates, and as man shares the characteristic structure of his cerebrum (the organ of thought) with the anthropoid apes, his psychic life also must have the same origin as theirs.

If we appreciate the full weight of these morphological and physiological facts, and put a proper phylogenetic interpretation on the observations of embryology, we see that the older idea of the personal immortality of the human soul is scientifically untenable. Death puts an end, in man as in any other vertebrate, to the physiological function of the cerebral nervous, the countless microscopic ganglionic cells, the collective activity of which is known as "the soul." I have shown this fully in the eleventh chapter of my *Study of the Universe*.

## CHAPTER XXV.

### EVOLUTION OF THE SENSE-ORGANS

THE sense-organs are doubtless among the most important and interesting parts of the human body, they are the organs by means of which we obtain our knowledge of objects in the surrounding world. *Mit tel seines seines gutes non poter facit se seus.* They are the first organs of the life of the soul. There is no other part of the body in which we discover such elaborate anatomical structures, co-operating with a definite purpose; and there is no other organ in which the wonderful and purposive structure comes so clearly to control us to submit a Creator and a preconceived plan. Hence we find special efforts made by dualists to draw our attention here to the "wisdom of the Creator" and the design visible in his works. As a matter of fact, you will discover, on mature reflection, that on this theory the Creator is at bottom only playing the part of a clever mechanic or watch-maker; all these foolish teleological ideas of Creator and creation are

based, in the long run, on a similar childish anthropomorphism.

However, we must grant that at the first glance the teleological theory seems to give the simplest and most satisfactory explanation of these purposive structures. If we merely examine the structure and functions of the most advanced sense-organs, it seems impossible to explain them without postulating a creative act. Yet evolution shows us quite clearly that this popular Max is totally wrong. With the assistance we discover that the purposive and remarkable sense-organs were developed, like all other organs, without any preconceived design—developed by the same mechanical process of natural selection, the same constant correlation of adaptation and heredity, by which the other purposive structures in the animal frame were slowly and gradually brought forth in the struggle for life.

Like most other Vertebrates, man has six sensory organs, which serve for sight

different classes of sensations. The skin serves for sensations of pressure and temperature. This is the oldest, lowest, and vaguest of the sense-organs; it is distributed over the surface of the body. The other sensory activities are localized. The visual sense is bound up with the skin of the external visual organ, the sense of taste with the mucous lining of the mouth (tongue and palate), and the sense of smell with the mucous lining of the nasal cavity. For the two most advanced and most highly differentiated sensory functions there are special and very elaborate mechanical structures—the eye for the sense of sight, and the ear for the sense of hearing and space (equilibrium).

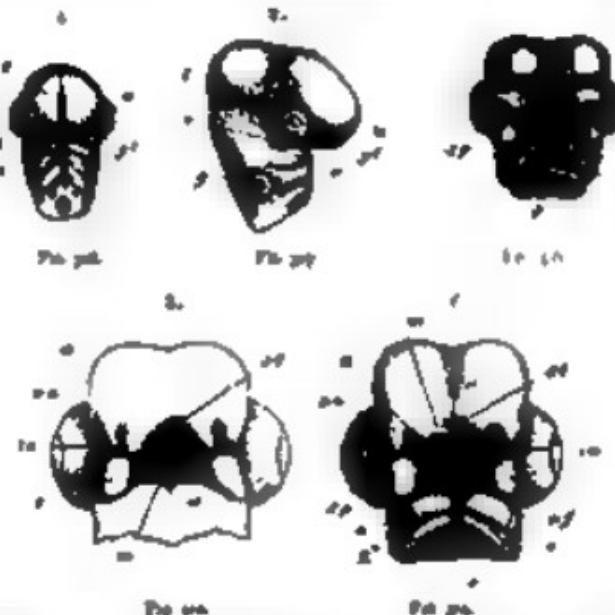
Comparative anatomy and physiology teach us that there are no differentiated sense-organs in the lower animals; all their sensations are received by the surface of the skin. The undifferentiated skin-layer or ectoderm of the Gastrula is the simple stratum of cells from which the differentiated sense-organs of all the Metazoa (including the Vertebrates) have been evolved. Starting from the assumption that necessarily only the superficial parts of the body, which are in direct touch with the outer world, could be concerned in the origin of sensations, we can see at once that the sense-organs also must have arisen there. This is really the case. The chief part of all the sense-organs originates from the skin-sense-layer, partly directly from the body-plat, partly from the brain, the foremost part of the medullary tube, what is left separated from the body-plat. If we compare the embryonic development of the various sense-organs, we see that they all make their appearance in the simplest conceivable form: the rudimentary contrivances that make the higher sense-organs among the most remarkable and elaborate structures in the body developing only gradually. In the fully hypothetical explanation of their comparative anatomy and ontogeny achieve their greatest triumph. But at first all the sense-organs are merely parts of the skin in which sensory nerves expand. These nerves themselves were originally of a homogeneous character. The different functions or specific energies of the differentiated sense-organs were only gradually developed by division of labor. At the same time, their simple terminal expansions in the skin were converted

The great importance of these historical facts in connection with the life of the soul is not difficult to see. The whole philosophy of the future will be transformed as soon as psychology takes cognizance of these genetic phenomena and makes them the basis of its speculations. When we examine impartially the memoirs of psychology that have been published by the most distinguished evolutionary philosophers and are still widely distributed, we are astonished at the number of it's which the authors raise their sky-metaphysical speculations, regardless of the numerous anatomical facts that completely refute them. Yet the science of evolution, in conjunction with the great advance of the comparative anatomy and physiology of the sense-organs, provides the one sound empirical basis of a natural psychology.



have already considered (p. 229) the organ of touch and temperature in the skin. I need only add that in the carapace of man and all the higher Vertebrates countless microscopic sense-organs develop, but the precise relation of these to the sensations of pressure or relaxation, of warmth and cold, has not yet been explained. Organs of this kind, in or on which sensory cutaneous nerves terminate, are the "tactile corpuscles" (or the

capilli to which these parts belong (Chapter XXVII.) I will only point out for the present that the mucous coat of the tongue and palate, in which the gustatory nerves end, originates from a part of the outer skin. As we have seen, the whole of the mouth-cavity is formed, not as a part of the gut-tube proper, but as a pit-like fold of the outer skin (p. 139). Its mucous lining is therefore formed, not from the visceral, but from the cutaneous



Figs. 1, 2, and 3.—Head of a chick embryo, three days old. pit. front. v. n. pit. from the right. = rad. mandib. (mandibular pit.) = retro-mandib. gang., pars. genito-sacra (genito-sacral pit.) = pit. brain; pit. oculi, = processus opticus pit. = processus hypophysis pit. of the first gill-folds.

The yolk.—Head of a chicken embryo, four days old from below. = vitell. pit. = supra-yolk process of the hind-gut. A hollowed process of bone. It is said different, of altered bones of yolk, & yolk.

Figs. 4, 5, and 6.—Head of chick embryos 1, 2, 3 days old from the roof of the mouth, pit. from the beginning of the RA. with. Labels as in Fig. 1, except 1. Sp. br., = pit. brain; 2. process. of nasal furrow; 3. frontal process, at mouth. (From Müller.) Figs. 5 and 6 are magnified to the same extent.

Tactile corpuscles) and end-balls. We find similar corpuscles in the organs of the sexual sense, the male penis and the female clitoris; they are processes of the skin, the development of which we will consider later (together with the rest of the sexual parts, Chapter XXIX.). The evolution of the organ of taste, the tongue and palate, will also be treated later, together with that of the olfactory

layer, and the taste-cells at the surface of the tongue and palate are not products of the gut-lining layer, but of the skin-sense layer.

This applies also to the mucous lining of the olfactory organ, the nose. However, the development of this organ is much more interesting. Although the nose seems superficially to be simple and single, it really consists, in man and all

other Gnathostomes, of two completely separated halves, the right and left cavities. They are divided by a ventral partition, so that the right nostril leads into the right cavity alone and the left nostril into the left cavity. They open internally (and separately) by the posterior nasal apertures into the pharynx, so that we can get direct into the gutlet through the nasal passages without touching the mouth. This is the way the air usually passes in respiration; the nostrils being closed, it goes through the nose into the gutlet, and through the larynx and bronchial tubes into the lungs. The nasal cavities are separated from the mouth by the bidental bony plate, to which is attached below (as a dependent process) the soft palate with the uvula. In the upper and blander parts of the nasal cavities the olfactory nerve, the first pair of cerebral nerves, expands in the mucous coil which clothes them. The terminal branches of it spread partly over the septum (partition), perch on the side-walls of the internal nostrils, to which are attached the turbinated bones. These bones are much more developed in many of the higher mammals than in man, but there are three of them in all mammals. The sensation of smell arises by the passage of a current of air containing odorous matter over the mucous lining of the cavities, and stimulating the olfactory cells of the membranes.

Man has all the features which distinguish the olfactory organ of the mammals from that of the lower Vertebrates. In all essential points the human nose entirely resembles that of the Catarrhine Apes, some of which have quite a robust external nose (compare the face of the long-nosed apes). However, the first structure of the olfactory organ in the human embryo gives an indication of the future simple proportions of our catarrhine nose. It has the form in which we find it permanently in the fishes—a couple of simple depressions in the skin at the outer surface of the head. We find these blind olfactory pits in all the fishes; sometimes they lie near the eyes, sometimes more forward at the point of the mouth, sometimes lower down, near the mouth (Fig. 290).

This first rudimentary structure of the double nose is the same in all the Gnathostomes; it has no connection with the primitive mouth. But even in a median

region to make its appearance, a furrow in the surface of the skin running from each side of the nasal pit to the nearest corner of the mouth. This furrow, the nasal groove or furrow (Fig. 295 a), is very important. In many of the sharks, such as the *Squalus*, a special process of the frontal skin, the nasal fold or internal nasal process, is formed internally over the groove (a, a'). In contrast to this the outer edge of the furrow rises in an "external nasal process." As the two processes meet and coalesce over the



FIG. 295.—Frontal section of the head and neck of a human embryo, back half much larger than the front. (From W. H. P. The vertical section is the dorsal plane, from left to right; it is so constructed that we see the nasal pit in the upper third of the figure and the eye at the side. In the middle third the nostriles open into the gutlet; left nostril is enclosed in the large shield-like premaxillary bone; and the medial tube and the rudimentary tongue.

nasal groove in the Diplopoda and Amphibia, it is converted into a canal, the nasal canal. Henceforth we can pass back from the external pit through the nasal canal direct into the mouth, which has been formed quite independently. In the Diplopoda and the lower Amphibia the inferior aperture of the nasal canal lies in front (instead of the lips); in the higher Amphibia it is right behind. Finally, in the three higher classes of Vertebrates the primary mouth-cavity is

palate-rear has two distinct cavities—the upper (secondary) nasal cavity and the lower (secondary) mouth-cavity. The nasal cavity in turn is divided by the separation of the vertical septum into two halves—right and left.

Comparative anatomy shows us to-day, in the series of the dimly-armed Vertebrates, from the fishes up to man, all the different stages in the development of the nose, which the advanced character-stage of the higher mammals has passed through at various periods in the course of its phylogeny. It first appears in the embryo of man, and the higher Vertebrates, in which the adult features persist throughout life. At an early stage, before there is any trace of the characteristic human face, a pair of small pits are formed in the head over the original mouth-region; these were first described by Baer, and rightly called the "olfactory pits" (Fig. 300 a, just as



FIG. 300.—Diagrammatic section of the early embryo. With the primordial "frontal process" are seen the two olfactory pits (*n*) and the upper oral cavity, the latter being divided by the nasal process (*s*) into two halves (in. = line of section).

These primitive nasal pits are quite separated from the mouth-region, which sits brightness as a middle depression in the skin, in front of the bloodless end of the gut. Both the pair of nasal pits and the single mouth-pit (Fig. 300 a) are clothed with the horny skin. The original separation of the former from the latter is, however, promptly established, a process forming above the mouth-pit—the "frontal process" (Fig. 300 a). Its outer edge turns to the right and left in the shape of two lateral processes. These are the inner nasal processes or folds (*m*). Opposite to them a parallel ridge is formed on either side between the eye and the nasal pit; these are the outer nasal processes (*s*, *m*). Thus between the inner and outer nasal processes a groove-like depression is formed on either side, which leads from the oral

pit towards the mouth-pit (*m*): this groove is, as the reader will guess, the nose and furrow or groove that we have already seen in the shark (Fig. 301). As the naso-lateral ridges of the inner nasal process bend towards each other and join above the nasal groove, this is converted into a tube, the primitive nasal canal. Hence the name of nose and all the other Avescines pointing at this embryonic stage of a couple of narrow tubes, the nasal canals, which lead from the outer surface of the forehead into the rudimentary mouth. This process should now convince the reader in which we find the nose permanently in the Diplopoda and Annelids.

A cone-shaped突起, which grows from below upwards the upper ends of the two nasal processes and joins with them, plays no important part in the conversion of the open nasal groove into the closed canal. This is the upper-jaw process (Fig. 301-310). Below the mouth-pit are the gill-slits, which are separated by the gill-clefts. The first of these gill-slits, and the most important for our purpose, which we may call the maxillary (max) arch, forms the diastema of the jaws. Above on the head a small process grows out of the first gillarch, this is the upper-jaw process. The low gillarch half-develops a maxilla at one of its later ends, the "Maxilla cartilaginea" (named after its structure), on the outer surface of which the bone jaw is formed (Fig. 301-310). The upper-jaw process forms the chief part of the skeleton of that jaw, the palato bone, and the pterygoid bone. On the outer side is afterwards formed the upper-jaw bone, in the maxillary series, while the middle part of the skeleton of the upper jaw, the maxillary, develops from the foremost part of the frontal process.

The two upper-jaw processes are of great importance in the further development of the face. From them is formed, growing into the primitive mouth-cavity, the important longitudinal partition (the palate) that divides the former into two distinct cavities. The upper cavity, into which the nasal canals open, now develops into the nasal cavity, the air-passages and the organ of smell. The lower cavity forms the permanent secondary mouth (Fig. 322 m), the food-passage and the organ of taste. Both the upper and lower cavities open behind into the gut (pharynx). The last

palate that separates them is formed by the joining of two lateral halves, the horizontal plates of the two upper-maxillary processes, or the palate-plate (Fig.). When these do not, sometimes, completely join in the middle, a longitudinal cleft remains, through which we can penetrate from the mouth straight into the nasal cavity. This is the malformation known as "cleft's throat." "Harelip" is the lesser form of the same defect. At the same time as the horizontal partitions of the hard palate a vertical partition is formed by which the single nasal cavity is divided into two apertures—a right and left half (Fig. 312 n, n).

As, growing forwards from behind. The characteristic human nose is formed very late. Much stress is at times laid on this organ as an exclusive privilege of man. But there are apes that have similar noses, such as the long-nosed ape.

The evolution of the eye is not less interesting and instructive than that of the nose. Although this noblesse of the sensory organs is one of the most delicate and purposive on account of its optic perfection and remarkable structure, it nevertheless develops, without perceptible stages, from a simple process of the outer germinal layer. The fully-formed human eye is a round capsule, the



FIG. 312.

FIGS. 312 AND 314.—Diagram part of the body of a human embryo, ventral view of an inch long of the fifth month. FIG. 312 from the left, FIG. 314 from the right. The eye is seen in the figure by front left lateral and slightly superior before and to the clavicle bone. Head and upper lip undergo a proportion, in the first, to the face, and especially to the lower lip. (From Haeckel's "Kunstformen der Natur," Vol. I.)



FIG. 314.

The double nose has now acquired the characteristic form that man shares with the other mammals. Its further development is easy to follow; it consists of the formation of the inner and outer processes of the walls of the two cavities. The external nose is not formed until long after all these essential parts of the internal organ of smell. The first traces of it in the human embryo are found about the middle of the second month (Figs. 313-316). As can be seen in any human embryo during the first month, there is at first no trace of the external nose. It only develops afterwards from the foremost (front) part of the primitive

eye-ball (Fig. 317). This lies in the bony cavity of the skull, surrounded by protective fat and motor muscles. The greater part of it is taken up with a translucent, transparent gelatinous substance, the corpus vitreum. The crystalline lens is fixed into the anterior surface of the ball (Fig. 317 f). It is a biconvex, incapsulated body, the most important of the refractive media in the eye. Of this group we have, besides the corpus vitreum and the lens, the watery fluid (*humor aquosus*) that is found in front of the lens (at the letter m in Fig. 317). These three transparent refractive media, by which the rays of light that

enter the eye are broken up and re-focused, are enclosed in a solid round capsule, composed of several different coats, something like the concentric layers of an onion. The anterior and

posterior) to the eye, penetrates its outer envelopes, and then spreads out like a net between the choroid and the corpus vitreum. Between the retina and the choroid there is a very delicate membrane, which is usually (but wrongly) associated with the latter. This is the black pigment-mucous-membrane (*a*). It consists of a single stratum of graceful, hexagonal, regularly-jointed cells, full of granules of black-coloured matter. This pigment-mucous-clathræ, not only the inner surface of the choroid proper, but also the blind surface of its anterior muscular continuation, which covers the edge of the lens as far as a circular membrane, and arrests the rays of light at the sides. This is the well-known *iris* of the eye (*b*), coloured differently in different individuals (blue, grey, brown, etc.); it forms the anterior border of the choroid. The circular opening that is left in the middle is the *pupil*, through which the rays of light penetrate into the eye. At the point where the iris borders the latter is very thick, and forms a delicate crown of folds (*c*), which surrounds the edge of the lens with about twenty large and many smaller rays *frons utrumque*.

At a very early stage a couple of pear-shaped vesicles develop from the forepart of the first cerebral vesicle in the embryo of man and the other Craniotes (Figs. 322, 323, 324). These growths are the primary optic vesicles. They are at first directed outward and forward, but presently grow downward, so that, after the complete separation of the five cerebral vesicles, they lie at the base of the intermedio-brain. The upper cavities of these pear-shaped vesicles, which soon attain a considerable size, are openly connected with the ventricle of the intermedio-brain by their hollow stems. They are covered externally by the epidermis.

At the point where these vesicles are direct contact with the more curved part of the primary optic vesicle there is a thickening (*d*) and also a depression (*e*) of the horny plate (Figs. 318, 319). This pit, which we may call the lens-pit, is converted into a closed sac, the thick-



Fig. 322.—Part of a human embryo, age 10 weeks, showing the initial process of eye formation. The upper layer of the epidermis has been removed.

thickest of these envelopes is the white sclerotic coat of the eye. It consists of tough white connective tissue. In front of the lens a circular, strongly-curved, transparent plate is fixed into the sclerotic, like the glass of a watch—the cornea (*f*). At its outer surface the cornea is covered with a very thin layer of the epidermis, this is known as the conjunctiva. It goes from the corner over the inner surface of the eye-lids, the upper and lower folds which we draw over the eye in closing it. At the inner corner of the eye we have a rudimentary organ in the shape of the toe of a child (*lower*) eyelid, which is greatly developed, as "nictitating (winking) membrane," in the lower Vertebrates (p. 32). Underneath the upper eye-lid are the lacrymal glands, the product of which, the lacrymal fluid, keeps the outer surface of the eye smooth and clear.

Immediately under the sclerotic we find a very delicate, dark-red vascular, very rich in blood-vessels—the choroid coat—and inside this the retina (*g*), the expansion of the optic nerve (*h*). The latter is the second cerebral nerve. It proceeds from the optic thalamus (by several cerebral



Fig. 323.—Part of a human embryo, age 12 weeks old (from Gegenbaer).

walled lens-vehicle ( $\gamma_2$ ,  $\beta_2$ ), the thick edge of the pit joining together above it. In the same way in which the medullary tube separates from the outer germinal layer, we now see this lens-arc sever itself entirely from the horny plate ( $\beta_3$ ), its source of origin. The hollow of the arc is afterwards filled with the cells of its thick walls, and thus we get the solid crystalline lens. This is, therefore, a purely epidermic structure. Together with the lens the small underlying piece of cuticle-plate also severs itself from the skin.

As the lens-separates from the cuticle-plate and grows larger, it necessarily hollows out the contiguous primary optic vesicle (Fig. 318,  $\gamma$ - $\delta$ ). This is done in just the same way as the invagination of the Mantle, which gives rise to the gutrula in the amphioxus (Fig. 318 C-F). In both cases the hollowing of the closed vesicle at one side goes so far that at last the inner, folded part touches the outer, not folded part, and the cavity disappears. As in the gutrula the first part is converted into the endoderm and the latter into the ectoderm, so in the invagination of the primary optic vesicle the retina ( $r$ ) is formed from the first (inner) part, and the black pigment membrane ( $p$ ) from the latter (outer, non-invaginated) part. The bulk of the primary optic vesicle is converted into the optic nerve. The lens ( $\beta_2$ ), which has no important part in this process, lies at first directly on the non-invaginated part, or the retina ( $r$ ). But they soon separate, a new structure, the corpus vitreum ( $\gamma_2$ ), growing between them. While the lenticular arc is being detached and is causing the invagination of the primary optic vesicle, another invagination is taking place from below; this proceeds from the superficial part of the skin-fibres over—the corium of the head. Behind and under the lens a lens-shaped processes from the cuticle-plate (Fig. 319  $\beta$ ), follows out the cup-shaped optic vesicle below, and presents between the lens ( $\gamma_2$ ) and the retina ( $r$ ). In this way the optic vesicle acquires the form of a head.

Finally, a complete fibrous envelope, the fibrous capsule of the eye-ball, is

formed about the secondary optic vesicle and its stem (the secondary optic nerve). It originates from the part of the head-plate which immediately encloses the eye. This fibrous envelope takes the form of a closed round vesicle, surrounding the whole of the ball and pushing between the lens and the horny plate at the outer side. The round wall of the capsule thus divides into two different membranes by surface-clawage. The lower membrane becomes the choroid or vascular coat, and in front the ciliary process and iris. The outer membrane is



FIG. 319.—The frog's eye in section. 1, Optic nerve; 2, optic vesicle; 3, retina; 4, pigment membrane; 5, lens; 6, fibrous capsule; 7, iris; 8, ciliary process; 9, conjunctiva; 10, skin; 11, cornea. (From Hertwigs "Optogenesie," a general treatise on the eye, 4 Pfeil's comic, yellow tip of the retina.) (From Hertwigs)

converted into the white protective or sclerotic coat—in front, the transparent cornea. The eye is now formed in all its essential parts. The further development—the complicated differentiation and composition of the various parts—is a matter of detail.

The chief point in this remarkable evolution of the eye is the circumstance that the optic nerve, the retina, and the pigment membrane originate really from a part of the brain—an outgrowth of the interventricular brain—while the lens, the chief refractive body, develops from the outer skin. From the skin—the horny

plate—also arises the delicate conjunctiva, which afterwards covers the outer surface of the eyeball. The lacrimal glands are remodeled growths from the conjunctiva (Fig. 326). All these important parts of



FIG. 326.—Eye of the chick: *1*, at 10 days; *2*, at 12 days; *3*, at 14 days. *A*, lens; *B*, retina; *C*, choroid; *D*, iris; *E*, optic nerve; *F*, fundus. (From a series of photographs by G. R. Lewis, reproduced from a paper on the development of the eye of the chick, by G. R. Lewis and J. W. S. Thompson, in the *Journal of Anatomy*, 1908, 42, p. 226.)

the eye are products of the outer germinal layer. The remaining parts—the corpus vitreum (with the vascular capsule of the lens), the choroid (with the iris), and the sclerotic (i.e., the cornea)—are formed from the middle germinal layer.

The outer protection of the eye, the eye-lids, are merely folds of the skin, which are formed in the third month of human embryonic life. In the fourth month the upper eyelid reaches the brow, and the eye remains covered with them until birth. As a rule, they open wide shortly before birth (sometimes only after birth). Our primate ancestors had a third eyelid, the nictitating membrane, which was drawn over the eye from its lateral angle. It is still found in many of the Selachii and Amniotes. In the apes and man it has degenerated, and there is now only a small relic of it at the inner corner of the eye, the sacral fold, a useless cutaneous organ (cf. p. 322). The apes and man have also lost the Harderian gland that opened under the nictitating membrane; we find this in the rest of the mammals, and the birds, reptiles, and amphibia.

The peculiar embryonic development of the vertebrate eye does not enable us to draw any definite conclusion as to its obscure phylogeny; it is clearly exogenetic to a great extent, as shown by the reduction and enlargement of its original features. It is probable that many of the earlier stages of its phylogeny have disappeared without leaving a trace,

it can only be said positively that the peculiar exogeny of the complicated optic apparatus in man follows just the same laws as in all the other Vertebrates. Their eye is a part of the fore brain, which has grown forward towards the skin, not an original cutaneous sense-organ, as in the Invertebrates.

The vertebrate ear resembles the eye and nose in many important respects, but is different in others, in its development. The auditory organ in the fully-developed man is like that of the other mammals, and especially the apes, in the main features. As in them, it consists of two chief parts—an apparatus for conducting sound (external and middle ear) and an apparatus for the sensation of sound (internal ear). The external ear opens in the skull at the side of the head (Fig. 327 *a*). From this point the external passage (*b*), about an inch in length, leads into the head. The inner end of it is closed by the tympanum, a vertical, but not quite upright, thin membrane of an oval shape (*c*). This tympanum separates the external passage from the tympanic cavity (*d*). This is a small cavity filled with air, in the temporal bone; it is connected with the mouth by a special tube.

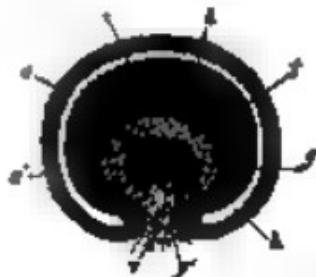


FIG. 327.—External ear and tympanum: *a*, side of the head; *b*, external ear; *c*, tympanum (the drum, the dark wall of which is as thick as the diameter of the central canal); *d*, tympanic cavity (connected by a short, blind canal, a vascular loop (pressing behind the base of the tympanum) which opens by means of the eustachian tube). Between, peritoneal layer of the preauricular vesicle, a peritoneal membrane (thin, undifferentiated layer of cells). A space between stroma and peritoneal membrane (residue of the cavity of the primary optic vesicle).

This tube is rather longer, but much narrower, than the outer passage, leads obliquely from the anterior wall of the tympanic cavity, and opens in the throat below, behind the gullet.

openings. It is called the Eustachian tube (*e.*); it serves to equalize the pressure of the air within the tympanic cavity and the outer atmosphere that enters by the external passage. Both



FIG. 320.—The human ear. *Left ear*:—*1*, External ear; *2*, skin of ear; *3*, pinna; *4*, tympanum; *5*, malleus; *6*, incus; *7*, stapes; *8*, the three joints of the auditory ossicles; *9*, cochlea; *10*, saccule; *11*, the three semicircular canals; *12*, the vestibule; *13*, acoustic nerve.

the Eustachian tube and the tympanic cavity are lined with a thin mucous coat, which is a direct continuation of the mucous lining of the throat. Inside the tympanic cavity there are three small bones which are known (from their shape) as the hammer, anvil, and stirrup (Fig. 320, *f*, *g*, *h*). The hammer (*g*) is the flattest, next to the tympanum. The anvil (*h*) lies between the other two, above and inside the hammer. The stirrup (*f*) lies inside the anvil, and touches with its base the outer wall of the internal ear, or vestibular vesicle. All these parts of the external and middle ear belong to the apparatus for conducting sound. Their chief task is to convey the waves of sound through the thick wall of the head to the fluid-lying vestibular vesicle. They are not found at all in fish. In them the waves of sound are conveyed directly by the wall of the vesicle to the vestibular vesicle.

The internal apparatus for the conduction

of sound, which receives the waves of sound from the conducting apparatus, consists in man and all other mammals of a closed auditory vesicle filled with fluid and an auditory nerve, the ends of which expand over the wall of this vesicle. The vibrations of the sound-waves are conveyed by these media to the nervous system. In the labyrinthine water that fills the auditory vesicle there are small stones at the points of entry of the acoustic nerves, which are composed of groups of microscopic calcareous crystals (otoliths). The vestibular organ of most of the Invertebrates has substantially the same composition. It usually consists of a closed vesicle, filled with fluid, and containing epithelia, with the acoustic nerve expanding on its wall. But, while the auditory vesicle is usually of a simple round or oval shape in the Invertebrates, it has in the Vertebrates a special and curious structure, the labyrinth. This elaborated labyrinth is enclosed in a bony capsule of the same shape, the osseous labyrinth (Fig. 321), and this lies in the middle of the porous bone of the skull. The labyrinth is divided into two vesicles in all the Craniota. The larger one is called the vestibule, and has three curved appendages, called the "semicircular canals" (*c*, *s*, *a*). The smaller vesicle is called the cochlea, and is connected with a peculiar appendage, with (in man and the higher mammals) a spiral form resembling like a snail's shell, and therefore called the cochlea (*m*; *coch.*). On the thin wall of this delicate labyrinth the acoustic nerve, which comes from the after-brain, spreads out in most elaborate fashion. It divides into two main branches—a cochlear nerve (for the cochlea) and a vestibular nerve (for the rest of the labyrinth). The former appears to have more to do with the quality, the latter with the quantity, of the acoustic sensations. Through the cochlear nerve we know the height and timbre, through the vestibular nerve the intensity, of sound.

The first structure of this highly elaborate organ is very simple in the embryo of man and all the other Craniota, it is a



FIG. 321.—The human labyrinth. *Left ear*:—*1*, vestibule; *2*, cochlea; *3*, anterior canal; *4*, posterior canal; *5*, lateral canal; *6*, round窗.

pit-like depression in the skin. At the back part of the head at both sides, near the after brain, a small thickening of the horny plate is formed at the upper end of the second gill-disk (Fig. 320 A & B). This sinks into a sort of pit, and covers from the epidermis, just as the lens of the eye does. In this way it is formed at each side, directly under the horny plate of the back part of the head, a small vesicle filled with fluid, the primitive auditory vesicle, or the primary labyrinth. As it separates from its source, the horny plate, and presses inwards and backwards into the skull, it changes from round to pear-shaped (Figs. 320 B & A, 323 a). The outer part of it is lengthened into a thin stem, which at first still exists between by a narrow canal. This is the labyrinthic appendage (Fig. 320 A'). In the lower Vertebrates it develops into a special cavity filled with

secreted in the shape of simple pouch-like invaginations of the utricle (as in *Ascidia*). The edges join together in the middle part of each fold, and separate from the utricle, the two ends remaining in open connection with its cavity. All *Cyclostomes* have these three canal-like canals, whereas among the Cyclo-stomes the lampreys have only two and the hag-fishes only one. The very complex structure of the cochlea, one of the most elaborate and wonderful outcomes of evolution. In the mammal body develops originally in very simple fashion as a stalk-like projection from the sacculus. As Hesse and Retzius have pointed out we find the successive ontogenetic stages of its growth represented particularly in the species of the higher Vertebrates. The cochlea is wanting even in the Monotremes, and is restricted to the rest of the mammals and man.



Fig. 320. Development of the primary labyrinth of *Carassius*. (After Kowalevsky's figures.) A, External surface of the skull. B, Internal structure of the skull. C, Secondary vesicle or secondary labyrinth. D, Primary vesicle, or primary canal, as formed under the epidermis (From Kowalevsky).

calcareous crystals, which remain again permanently in some of the primitive fishes, and opens outwards in the upper part of the skull. But in the mammals the labyrinthic appendage degenerates. In these it has only a phylogenetic value as a rudimentary organ, with no actual physiological significance. The nucleus relic of it passes through the wall of the petrous bone in the shape of a narrow canal, and incloses the residual appendage.

It is only the inner and lower surfaces part of the separated auditory vesicle that develops into the highly complex and differentiated structure that is afterwards known as the secondary labyrinth. This vesicle divides at an early stage into an upper and larger and a lower and smaller section. From the one we get the saccule with the acochlear canals; from the other the cochlea and the vestibule (Fig. 320 d). The canals are

derived phylogenetically from an ordinary cutaneous nerve, and is of quite different origin from the optic and olfactory nerves, which both represent direct outgrowths of the brain. In this respect the auditory organ is essentially different from the organs of sight and smell. The acoustic nerve is formed from ectodermic cells of the hind brain, and develops from the nervous structure that appears at its dorsal limit. On the other hand, all the membranous, cartilaginous, and osseous coverings of the labyrinth are formed from the mesodermic levels.

The apparatus for conducting sound which we find in the external and middle ear of vertebrates develops quite separately from the apparatus for the sensation of sound. It is both phylogenetically and ontogenetically an independent sensory function, a later division to

the primary internal ear. Nevertheless, its development is not less interesting, and is explained with the more ease by comparative anatomy. In all the fishes and in the lower Vertebrates there is no



FIG. 241.—Embryonic skull of the hagfish (*Myxine glutinosa*), four weeks old, ventral surface, left half removed. 1, mouth; 2, nostrils; 3, 4, 5, 6, 7, the gills of the external ear; 4, oral cavity; 5, 6, 7, the three opercular openings. (From H. Müller and Franz Stärke, *Die Entwicklung der Larven und der Jungen des Haifischs*, 1887.)

special apparatus for conducting sound, no external or middle ear, they have only a labyrinth, an internal ear, which lies within the skull. They are without the tympanum and auditory cavity, and all its appendages. From time immemorial (see 41) the best few decades it seems that many of the fishes (of not all) cannot distinguish tones, since they seem to be wholly (if not exclusively) an organ for the sense of touch (or magnetism). If it is destroyed, the fishes lose their balance and fall in the opinion of most physiologists (and apply also to many of the invertebrates (including the marine mammals of the Vertebrates). The round vessels which are considered to be their auditory vesicles, and which originate as clefts, are supposed to be merely evaginations of the sacculus ("static vesicles" or statocysts").

The middle ear makes its first appearance in the amphibia class, where we find a tympanum, tympanic cavity, and Eustachian tube; these animals, and all terrestrial Vertebrates, certainly have the faculty of hearing. All these essential parts of the middle ear originate from the first gill-cleft and its surrounding parts: in the Selachii this remains throughout life an open squinting-hole, and lies between the first and second gill-clefts. In the embryo of the higher Vertebrates it closes up in the centre, and thus forms

the tympanic membrane. The outlying remainder of the first gill-cleft is the rudiment of the external meatus. From its inner part we get the tympanic cavity, and, further inward still, the Eustachian tube. Connected with this is the development of the three bones of the mammal ear from the first two gillarches; the hammer and anvil are formed from the first, the stirrup from the upper end of the second, gillarch.

Finally, the shell (pinna or concha) and external meatus (passage to the tympanum) of the outer ear are developed in a very simple fashion from the skin that covers the external aperture of the first gill-cleft. The shell rises in the shape of a circular fold of the skin, in which cartilage and muscles are afterwards formed (figs. 393 and 395). This organ is only found in the mammalian class. It is very rudimentary in the lowest forms, the Monotremes. In the others it is found at very different stages of development, and sometimes of degeneration. It is degenerate in most of the aquatic mammals. The majority of them have lost it altogether—for instance, the seals and whales and most of the seals. On the other hand, the whale is



FIG. 242.—The rudimentary meatus of the ear in the hagfish skull, a rising muscle of whitish, & thinning muscle of whitish, & thickening muscle of whitish, & large muscle of the body of dark red muscle, & small muscle of the body of dark red muscle, & muscle of the body of dark red muscle, & thinning muscle of whitish.

well developed in the great majority of the Monotremes and Placentalia; it receives and collects the waves of sound, and is equipped with a very pliable muscular apparatus, by means of which the place

can be turned freely in any direction and its shape be altered. It is well known how readily domestic animals—horses, cows, dogs, hares, etc.—raise their ears and move them in different directions. Most of the apes do the same, and our earlier ape ancestors were also able to do it. But our later simian ancestors, which we have in common with the anthropoid apes, abandoned the use of these muscles, and they gradually became rudimentary and useless. However, we possess them still (Fig. 322). In fact, some men can still move their ears a little backward and forward by means of the drawing and withdrawing muscles (*b* & *c*); with practice this faculty can be much improved. But no man can now lift up his ears by the raising muscle (*a*), or change the shape of them by the small inner muscles (*A*, *C*, *D*, *E*). These muscles were very useful to our ancestors, but are of no consequence to us. This applies to most of the anthropoid apes as well.

We also share with the higher anthropoid apes (gorilla, chimpanzee, and orang) the characteristic form of the human outer ear, especially the folded border, the bella, and the lobe. The lower apes have pointed ears, without folded border or lobe, like the other mammals. But Darwin has shown that at the upper

part of the folded border there is in many men a small pointed process, which most of us do not possess. In some individuals this process is well developed. It can only be explained as the relic of the original point of the ear, which has been turned inward in consequence of the curving of the edge. If we compare the plains savages and the various apes in this respect, we find that they present a consecutive series of degenerate structures. In the common arboreal ancestors of the anthropoids and man the degeneracy set in with the folding together of the pinnae. This brought about the bella of the ear, in which we find the significant angle which represents the relic of the salient point of the ear in our simian simian ancestors. Here again, therefore, comparative anatomy enables us to trace with certainty the human ear to the simian, but more developed, organ of the lower mammals. At the same time, comparative physiology shows that it was a more or less useful implement in the latter, but it is quite useless in the anthropoids and man. The conducting of the sound has scarcely been affected by the loss of the pinna. We have also in this the explanation of the extraordinary variety in the shape and size of the shell of the ear in different men; in this it resembles other rudimentary organs.

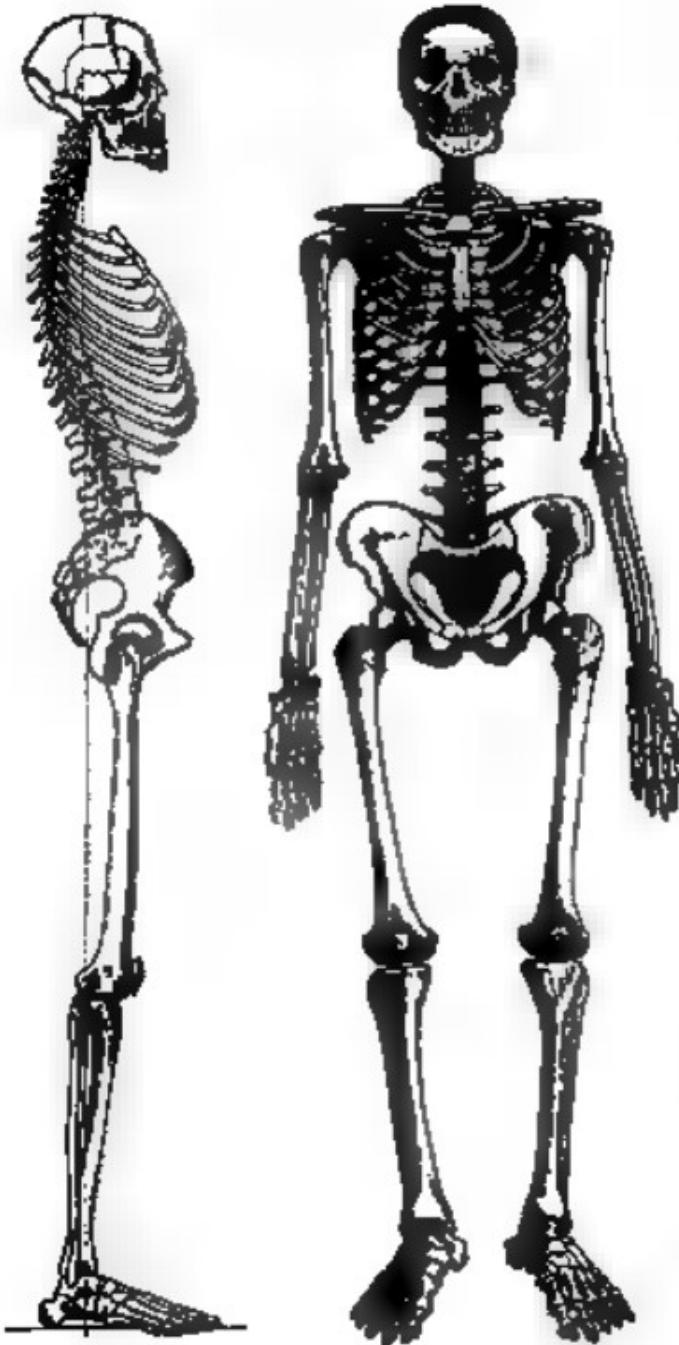
## CHAPTER XXVI.

### EVOLUTION OF THE ORGANS OF MOVEMENT

The peculiar structure of the locomotive apparatus is one of the features that are most distinctive of the vertebrate class. The chief part of this apparatus is formed, as in all the higher animals, by the active organs of movement, the muscles; in consequence of their contractility they have the power to draw up and shorten themselves. This affects the movement of the various parts of the body, and thus the whole body is conveyed from place to place. But the

arrangement of these muscles and their relation to the solid skeleton are different in the Vertebrates from the Invertebrates.

In most of the lower animals, especially the Platydes and Vermalia, we find that the muscles form a simple, thin layer of flesh immediately underneath the skin. This muscular layer is very closely connected with the skin itself; it is the same in the Mollusc shell. Even in the large division of the Articulata, the classes of insects, spiders, myriapods, and



insects, we find a similar feature, with the difference that in this case the skin forms a solid armour—a rigid cutaneous skeleton made of chitin (and also about carbonates of lime).



FIG. 325.—The human vertebral column, standing upright, front view, with the right side drawn.

In order to get a clear idea of the chief features of the development of the human skeleton, we need first examine its composition in the adult form (Fig. 325, the human skeleton seen from the right, Fig. 326, front view of the whole skeleton). As in other mammals, we distinguish first between the axial or dorsal skeleton and the skeleton of the limbs. The axial skeleton consists of the vertebral column (the skeleton of the trunk) and the skull (skeleton of the head); the latter is a peculiarly modified part of the former. As appendages of the vertebral column we have

the ribs, and of the skull we have the hyoid bone, the lower jaw, and the other products of the gillarches.

The skeleton of the limbs or extremities is composed of two groups of parts—the skeleton of the extremities proper and the zone-skeleton, which connects these with the vertebral column. The zone-skeleton of the arms (or fore-limbs) is the shoulder-girdle; the zone-skeleton of the legs (or hind-limbs) is the pelvic girdle.

The vertebral column (Fig. 327) in man is composed of thirty-three to thirty-five ring-shaped bones in a continuous series (above each other, in man's upright position). These vertebrae are separated from each other by elastic ligaments, and at the same time connected by joints, so that the whole column forms a firm and solid, but flexible and plastic, axial skeleton, moving freely in all directions. The vertebrae differ in shape and construction at the various parts of the trunk, and we distinguish the following groups in the series, beginning at the top: seven cervical vertebrae, twelve dorsal vertebrae, five lumbar vertebrae, five sacral vertebrae, and four to six caudal vertebrae. The uppermost, or those next to the skull, are the cervical vertebrae (Fig. 328); they have a hole in each of the lateral processes. There are seven of these vertebrae in man and around all the other mammals; even the seal is as long in this of the camel or giraffe, or as short as that of the mole or hedgehog.

This number, which has for centuries (due to adaptation), i. a strong proof of the common descent of the mammals; it cannot be explained by faithful heredity from a common stem-form, a primitive mammal with seven cervical vertebrae. Mammal species had been created separately, it would be more logical than nine, and the short-necked animals less cervical vertebrae. Next to them come the dorsal (or pectoral



FIG. 326.—A plan of the human vertebral column, front view. From a dried human subject. (From Anders.)

had been better imagined than nine, and the short-necked animals less cervical vertebrae. Next to them come the dorsal (or pectoral

vertebrae, which number twelve to thirteen (usually twelve) in man, and most of the other mammals. Each dorsal vertebra (Fig. 365) has at the side, connected by joining a couple of ribs, long bony arches that lie in and protect the wall of the chest. The twelve pairs of ribs, together with the connecting intercostal muscles and the sternum, which joins the ends of the right and left ribs in front, form the chest (thorax). In this strong and elastic frame are the lungs, and between them the heart. Next to the dorsal vertebrae comes a short but stronger section of the column, formed of five large vertebrae. These are the lumbar vertebrae (Fig. 366); they have no ribs and the hollow in the transverse process. To

FIG. 365.—Dorsal vertebrae from a human embryo, aged 16 weeks, showing the typical mammalian features of a prominent neural spine, a median sacrum, and the ventral process of the transverse process. (From Müller.)

succeeds the sacral bone, which is formed between the two halves of the pelvic girdle. The sacrum is formed of five vertebral, completely blended together. Finally, we have at the end a small rudimentary caudal column, the sacrum. This consists of a varying number (usually four, more rarely three, or five or six) of small degenerated vertebrae, and is a mere rudimentary organ with no actual physiological significance. Morphologically, however, it is of great interest as an irrefragable proof of the descent of man and the anthropoids from long-tailed apes. On no other theory can we explain the existence of this rudimentary tail. In the earlier stages of development the tail of the human embryo protrudes considerably. It afterwards atrophies; but the root of the atrophied caudal vertebrae and of the rudimentary muscles that remain in it remains permanently. Sometimes, in fact, the external tail is preserved. The older anatomists say that the tail is usually one vertebra longer in the human female than in the male (or four against five). Stellwach says it is the reverse.

In the human vertebral column there are usually thirty-three vertebrae. It is interesting to find, however, that the

womb often changes, one or two vertebrae dropping out or an additional one appearing. Often, also, a mobile rib is inserted at the junction of the first lumbar vertebra, so that there are then thirteen dorsal vertebrae, besides two cervical and four lumbar. In this way the contiguous vertebrae of the various sections of the column may take each other's places.

In order to understand the embryology of the human vertebral column we must first carefully consider the shape and connection of the vertebrae. Each vertebra, in general, has the shape of a seal-ring (Figs. 365-366). The thicker portion, which is turned towards the central side, is called the body of the vertebra, and forms a short massive disk; the thinner part forms a semi-circular arch, the so-called neck, and is turned towards the back. The arches of the successive vertebrae are connected by thin intervertebral ligaments in such a way that the cavity they collectively enclose represents a long canal. In this vertebral canal we find the trunk part of the central nervous system, the spinal cord. Its head part, the brain, is enclosed by the skull, and the skull itself is merely the uppermost part of the vertebral column, distinguishably modified. The base or ventral side of the vertebral canal corresponds originally to a number of developed vertebral bodies; its ventral or dorsal side to those combined upper vertebral arches.

While the solid, massive bodies of the vertebrae represent the real central axis of



FIG. 366.—Dorsal vertebrae of the human embryo, a lateral view. The sacrum, a median sacrum, a ventral view with a portion of the ribs (lower arch). (From Müller.)

the skeleton, the dorsal arches serve to protect the central canal they enclose. But similar arches develop on the ventral side for the protection of the viscera in the breast and belly. These lower or

ventral vertebral arches, proceeding from the ventral side of the vertebral bodies, form, in many of the lower Vertebrates, a canal in which the large blood-vessels are enclosed on the lower surface of the



Fig. 321.—Lateral view of a embryo in the midbrain stage. A part of the brain. (From Müller.)

vertebral column (spinae and caudal rods). In the higher Vertebrates the majority of these vertebral arches are lost or become rudimentary. But at the thoracic section of the column (by development later independent strong osseous arches, the *spinolatera*). In reality the ribs are merely large and independent lower vertebral arches, which have lost their original connection with the vertebral bodies.

If we turn from this anatomical survey of the composition of the column to the question of its development, I may refer the reader to earlier pages with regard to the first and most important period (pp. 145-148). It will be remembered that in the human embryo and that of the other vertebrates we find at first, instead of the segmented column, only a simple unsegmented cartilaginous rod. This solid but flexible and elastic rod is the axial rod (or the *chorda dorsalis*). In the lowest Vertebrates, the Ascidians, it retains this simple form throughout life, and permanently represents the whole internal skeleton (Fig. 325 c). In the Tunicates, also, the nearest invertebrate relatives of the Vertebrates, we meet the same chorda—transitorily in the passing larva till of the Ascidia, permanently in the Copepoda (Fig. 325 c). Undoubtedly both the Tunicates and Ascidia have inherited the chorda from a common unsegmented stem-form; and these ancient, long-existing ancestors of all the

vertebrates, we may hypothetical Prochordians.

Long before there is any trace of the skull, heart, etc., in the embryo of nearly any of the higher Vertebrates—at the early stage in which the whole body is merely a disk-shaped embryonic shield—there appears in the middle line of the shield, directly under the medullary furrow, the simple chorda. (Cf. Figs. 325-325 ab). It follows the long axis of the body in the shape of a cylindrical axial rod of elastic but firm composition, equally pointed at both ends. In every case the chorda originates from the dorsal wall of the primitive gut; the cells that compose it (Fig. 325 b) belong to the mesoderm (Figs. 325-325-325). At an early stage the chorda develops a transparent structureless sheath, which is secreted from its dots (Fig. 325 a). This chondriform sheath is often called the "inner chondro-sheath," and must not be confused with the real external sheath, the fibroblastic perichorda.

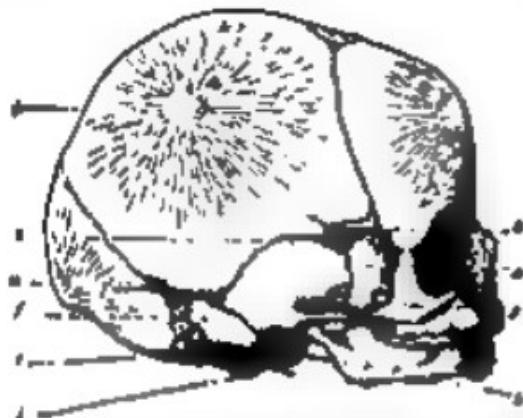
But this unsegmented primary axial skeleton is soon replaced by the segmented secondary axial skeleton, which we know as the vertebral column. The primitively plate (Fig. 325 a) differentiates from the unsegmented median part of the ventral layer of the chondro-musculum at each side of the chorda. As they grow round the chorda and enclose it they form the skeleton plate or *deuterostomous layer*—that is to say, the skeleton-forming stratum of cells, which provides the mobile foundation of the permanent vertebral column and skull (osculibut), in the hind-half of the embryo (the



Fig. 322.—Skull of a dogfish.

deuterostomous layer remains a continuous, simple, unfurrowed layer of tissue, and gradually enlarges into a thin-walled cavity enclosing the brain, the primordial skull. In the hind-half the provertebral

plate divides into a number of homogeneous, cubical, successive plates; these are the several primitive vertebrae. They are not numerous at first, but rapidly increase as the embryo grows larger (Figs. 153-155).



The segmented body wall of a primitive vertebrate. (From Sollner.) In the lower part of the body of the chick, as in the body of the fish, there is a narrow space between the dorsal plate and the body wall, bounded on the ventral side by the large process bone.  $\beta$  / The ventral bone is present (somite) / process bone;  $\gamma$  transverse bone;  $\delta$  dorsal part;  $\epsilon$  body;  $\zeta$  epiphysis;  $\vartheta$  large area of dermomyotome;  $\vartheta$  somite-nucleus of mesoderm bone.

In all the Craniotes the soft, undifferentiated cells of the mesoderm, which originally compose the stellate plate, are slowly converted for the most part into cartilaginous cells, and these secrete a firm and elastic intercellular substance between them, and form cartilaginous tissue. Like most of the other parts of the skeleton, the overbranched rudiments of the vertebral axis pass into a cartilaginous state, and in the higher Vertebrates this is afterwards replaced by the hard osseous tissue with its characteristic stellate cells (Fig. 6). The primary axial skeleton remains a simple chorda throughout life in the Actinians, the Cyclostomes, and the lowest fishes. In many of the other Vertebrates the chorda is more or less replaced by the cartilaginous tissue of the secondary perichordia that grows round it. In the lower Craniotes (especially the fishes) a more or less considerable part of the chorda is preserved in the bodies of the vertebrae. In the mammals it disappears for the most

part. By the end of the second month in the human embryo the chorda is merely a slender thread, running through the axis of the thick, cartilaginous vertebral column (Figs. 326, ch. 329, ch.). In the cartilaginous vertebral bodies themselves, which afterwards ossify, the slender remnant of the chorda gradually disappears (Fig. 329, ch.). But in the elastic intervertebral disks, which develop from the skeletal plate between each pair of vertebral bodies (Fig. 329, h), a relic of the chorda remains permanently. In the new-born child there is a large pear-shaped cavity in each intervertebral disk, filled with a gelatinous mass of cells (Fig. 331, a). Though this sharply defined, this gelatinous nucleus of the elastic cartilaginous disks persists throughout life in the mammals, but in the birds and most probably the last stage of the disks disappears. In the subsequent ossification of the two adjacent vertebrae the first deposit of "bony matter" ("first connective nucleus") takes place in the vertebral body immediately round the remainder of the chorda, and soon displaces it altogether. Then there is a nucleus formed in each



The segmented body wall of a primitive vertebrate. (From Sollner.) In the lower part of the body of the chick, as in the body of the fish, there is a narrow space between the dorsal plate and the body wall, bounded on the ventral side by the large process bone.  $\beta$  / The ventral bone is present (somite) / process bone;  $\gamma$  transverse bone;  $\delta$  dorsal part;  $\epsilon$  body;  $\zeta$  epiphysis;  $\vartheta$  large area of dermomyotome;  $\vartheta$  somite-nucleus of mesoderm bone.

half of the vertebral arch. The ossification does not reach the point at which the three vertebrae are joined until after birth. In the first year the two osseous halves of the arch unite; but it is much later—in the second to the eighth year—

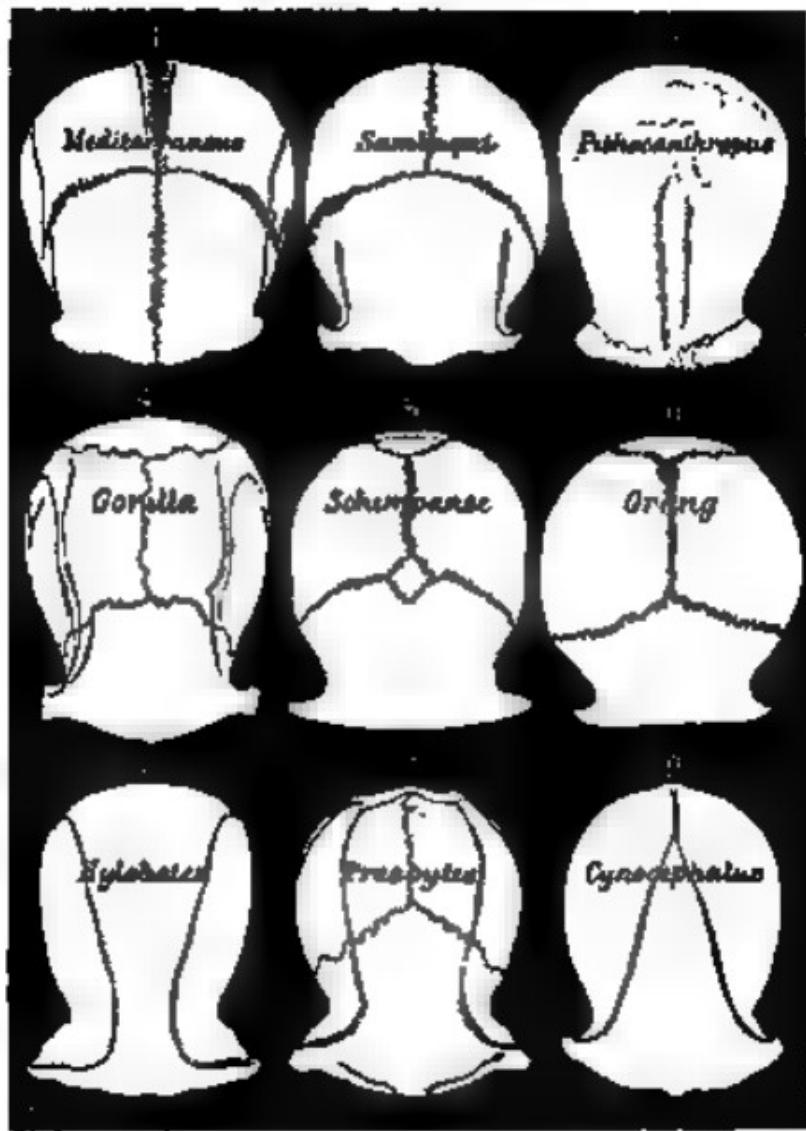


FIG. 282.—Diagrams of the brains of *Pithecanthropus*, *Sambawar*, *Australopithecus*, *Gorilla*, *Schimpanse*, *Orang*, *Hylobates*, *Presbytis*, and *Cynocephalus*.

that they connect with the common vertebral bodies.

The bony skull (*cranium*), the bony part of the respiratory and visceræ, develops in just the same way as the vertebral column. The skull forms a bony envelope for the brain, just as the vertebral canal does for the spinal cord; and as the brain is only a peculiarly differentiated part of the head, while the spinal cord represents the longer transsection of the originally homogeneous medullary tube, we shall expect to find

most above. The other thirteen bony parts form the facial skull, which is especially the bony envelope of the higher sense-organs, and at the same time encloses the entrance of the alimentary canal. The lower jaw is articulated at the base of the skull (usually regarded as the XXI. cervical bone). Behind the lower jaw we find the hyoid bone at the root of the tongue, also formed from the gillarches, and a part of the lower arches that have developed as "head-ribs" from the ventral side of the base of the cranium.



Fig. 331.

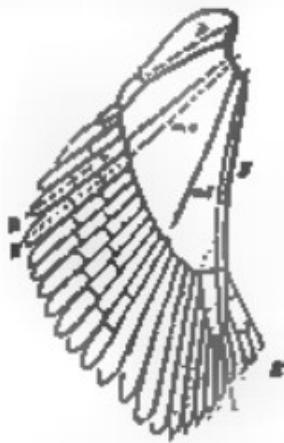


Fig. 332.

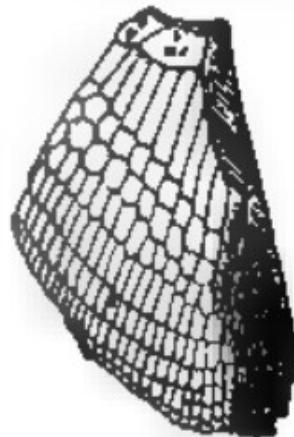


Fig. 333.

Fig. 331.—Illustration of the brachio-rib of *Gymnophion* (adult external surface). A, B, cartilaginous areas of the dorsal and ventral brachio-rib (from Goethe).

Fig. 332.—Illustration of the brachio-rib of an adult *Gymnophion*. The ribs of the median fin-rays, C, D, E, F, G, have disappeared for the most part, a few remain (Fig. 331, left). A, B, ribs of the dorsal brachio-rib, of which the dorsal and ventral brachio-rib (Fig. 333) are the remains. (From Goethe.)

Fig. 333.—Illustration of the brachio-rib of a young *Gymnophion*. The ribs of the median fin-rays have partly disappeared. The dorsal part on the right of the section that projects in the hypopharyngeal band of the higher Vertebrates. (A shallow, broad process of the first metapterygian bone, ventral of the mandible, the mesopterygian, a propterygian.) (From Goethe.)

that the nervous cord of the one is a special modification of the common envelope of the other. When we examine the adult human skull so itself (Fig. 332), it is difficult to conceive how it can be merely the modified fore-part of the vertebral column. It is an elaborate and extensive bony structure, composed of no less than twenty bones of different shapes and sizes. Some of these form the spacious shell that surrounds the brain, in which we distinguish the solid central base below and the curved dorsal

Although the fully-developed skull of the higher Vertebrates, with its peculiar shapes, its enormous size, and its complex construction, seems to have nothing in common with the ordinary vertebrae, nevertheless even the older comparative anatomists came to recognize at the end of the eighteenth century that it is really nothing else originally than a series of modified vertebrae. When Goethe in 1790 "picked up the skull of a dead victim from the sand of the Jewish cemetery at Tübingen, he excited at once

that the bones of the face also could be traced to vertebrae (like the three hindmost cranial vertebrae).” And when Oken, (without knowing anything of Goethe’s discovery) found at Hanau “a fine bejacketed skull of a bird, the thought flashed across him like lightning: ‘It is a vertebral column.’”

This famous vertebral theory of the skull has interested the most distinguished zoologists for more than a century: the chief representatives of comparative anatomy have devoted their highest powers to the solution of the problem, and the labour has spread far

beyond itself, and had compared the several bones that compose it with the several parts of the vertebra (Fig. 333); they thought they could prove in this way that the fully-formed mammal skull was made of from these to six vertebrae.

The older theory was refuted by simple and obvious facts, which were first pointed out by Huxley. Nevertheless, the fundamental idea of it—the belief that the skull is formed from the head-part of the perichordal axial skeleton, just as the brain is from the simple myelillary tube, by differentiated



FIG. 333.



FIG. 334.



FIG. 335.

FIG. 333.—Skeleto of the fore-leg of an amphipod. A appears dorsum; the brachium pars brachialis, B, the ulna, C, the radius, D, the carpus, E, the metacarpus, F, the phalanges. (From Gruber.)

FIG. 334.—Skeleto of gurnard's fore-leg. (From Huxley.)

FIG. 335.—Skeleto of human hand, left. (From Agassiz.)

beyond their circle. But it was not until 1872 that it was finally solved, after seven years' labour, by the comparative anatomist who surpassed all other experts of this science in the second half of the nineteenth century by the richness of his empirical knowledge and the accuracy and depth of his philosophic speculations. Carl Gegenbaur has shown, in his classic *Studies of the Comparative Anatomy of the Vertebrates* (third section), that we find the most solid foundation for the vertebral theory of the skull in the head-skeleton of the Selachii. Earlier anatomists had wrongly started from the

and modified—rethinked. The work now was to discover the proper way of applying this philosophic theory with an improved foundation, and it was reserved for Gegenbaur to achieve this. He first optima the phylogenetic path which leads, as in all morphological questions, leads most confidently to the goal. He showed that the primitive fishes (Figs. 349-352), the ancestors of all the Gnathostomes, still preserve permanently in the form of their skull the structure out of which the totaformed skull of the higher Vertebrates, including man, has been evolved. He further showed that the

branchial arches of the Selachii prove that their skull originally consisted of a large number of (at least nine or ten) provertebrae, and that the cerebral nerves had passed from the base of the brain entirely confirm this. These cerebral nerves are (with the exception of the first and second pair, the olfactory and optic nerves) merely modifications of spinal nerves, and are essentially similar to them in their peripheral expansion. The comparative anatomy of these cerebral nerves, their origin and their expansions, furnishes one of the strongest arguments for the new vertebral theory of the skull.

We have not space here to go into the details of Gegenbaur's theory of the

each side—the primitive upper jaw (*or Anulus quadratus*, *a*) and the primitive lower jaw (*b*); *c*, the hyoid bone (*II*); finally, *V-X*, six branchial arches in the narrower sense (*III-VIII*). From the anatomic features of these nine to ten cranial ribs or "lower vertebral arches" and the cranial nerves that spread over them, it is clear that the apparently simple cartilaginous primitive skull of the Selachii was originally formed from so many (at least nine) provertebrae or provertebrae. The blending of these primitive segments into a single capsule is, however, so ancient that, in virtue of the law of correlated heredity, the original dilatation seems to have dis-

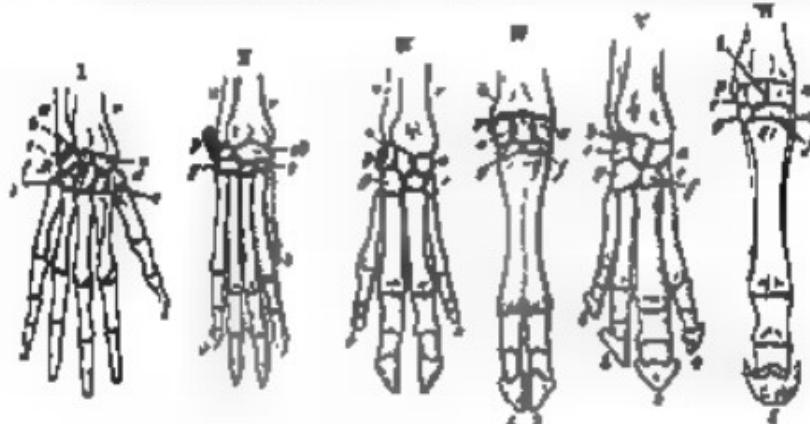




FIG. 202.

FIG. 202.—*Arm and hand of Gallus gallus domesticus.* FIG. 203.—*Gallus gallus domesticus super-*  
*ioris* (*domesticus*). FIG. 204.—*Gallus gallus domesticus*. FIG. 205.—*Gallus gallus domesticus*.

the the primitive cerebral vesicle, and correspond, like them, to a large number of metaclasses. That we have in the primitive skull of the mammals a greatly modified and transformed organ, and not at all a primitive formation, is clear from the circumstances that its original soft membranous form only assumes the cartilaginous character for the main part at the base and the sides, and membranous character at the roof. At this part the bones of the subsequent osseous shell develop an external coverings over the membranous structure, without an intermediate cartilaginous stage, as there is at the base of the skull. Thus a large part of the cranial base develops originally as covering bones from the surface, and only secondarily come into close touch with the primitive skull (Fig. 333). We have previously noted how the very rudimentary beginning of the skull is now so far removed ontogenetically from the "head-plate," and thus the fore end of the Chorda is enclosed in the base of the skull. (Cf. Fig. 129 and p. 116, 129 and 130.)

The physiology of the skull has made great progress during the last three decades through the joint achievements of comparative anatomy, embryology, and paleontology. By the judicious and comprehensive application of the physiognomical method (in the sense of Copeau) we have found the key to the great and important problems that arise from the thorough anthropological study of the skull. Another school of research, the school of what is called "exact craniology" (so the name of Virchow), has, however, made little effort to utilize this result. We may gratefully acknowledge all that this descriptive school has done in the way of accurately describing the various bones and measurements of the human skull, as compared with those of other mammals. But the real empirical material that it has accumulated in its extensive literature is mere dead and sterile tradition until it is verified and illumined by phylogenetic speculation.

Virchow confined himself to the most careful analysis of large numbers of human skulls and those of anthropoid mammals. He saw only the differences between them, and sought to express them in figures.

Without adducing a single solid reason, or offering any alternative explanation, he referred variation as we observed it to species. He played a most unfortunate

part in the controversy as to the significance of the fossil human skulls of Spy and Mauerthal, and the comparison of these with the skull of the Pithecanthropus (Fig. 333). All the interesting features of these skulls that clearly indicated the transition from the australopithecine to the man were declared by Virchow to be chance pathological variations. He said that the roof of the skull of Pithecanthropus (Fig. 333, 3) must have belonged to an ape, because so pronounced an orbital structure (the horizontal constriction between the outer edge of the eye-orbit and the temple) is not found in any human being, immediately anterior. Noting, however, in the skull of a Brazilian Indian (Fig. 333, 5), found in the Sambaquis of Santa, that this structure may be even deeper in man than in many of the apes, it is very



FIG. 333.—Transverse section of a skull of a baboon (Macacus) showing the internal structure of the base (modified after Virchow). A, brain; B, optic nerve; C, oculomotor nerve; D, maxillary nerve; E, mandibular nerve; F, hypoglossal nerve; G, vagus nerve; H, glossopharyngeal nerve; I, hypoglossal canal; J, foramen magnum; K, foramen rotundum; L, foramen ovale; M, foramen spinosum; N, foramen infraorbitalis; O, foramen opticum; P, foramen rotundum; Q, foramen ovale; R, foramen spinosum; S, foramen infraorbitalis; T, foramen opticum.

instructive in this connection to compare the skulls of the simian fauna from Africa of different genera. I have, therefore, arranged nine such skulls in Fig. 334, and reduced them to a common size.

We turn now to the branchial arches, which were regarded even by the earlier natural philosophers as "head-els." (Cf. Figs. 337-340). Of the four original arches of the mammals the first lies between the primitive mouth and the first gill-folds. From the base of this arch is formed the upper-jaw process, which joins with the inner and outer nasal processes on each side, in the manner we have previously explained, and forms the chief parts of the skeleton of the upper jaw (palate bone, pterygoid bone, etc.) (Cf. p. 264.) The remainder of the first branchial arch, which is now called by

way of contrast, the "ear" forms from its base ten (hammer and anvil), are converted into a hinge ; that is known, what is "Michel's cartilage," "ear" of the !

from the cellular

ring or secondary bone, the permanent, many lower jaw. From the first part or bone of the second branchial arch we get, to the maxilla, the third ossicle of the ear, the stapes ; and from the surrounding parts we get (in the adult) the malleus of the ear, the styloid process of the

third branchial arch is only cartilaginous at the forepart part, and here the body of the hyoid bone and its larger horns are formed at each side by the junction of the two halves. The fourth branchial arch is only found transiently in the mammal embryo as a rudimentary organ, and does not develop special parts, and there is no trace in the embryo of the higher Vertebrates of the posterior branchial arches (fifth and sixth pair), which are transferred to the Sacellum. They have been lost long ago. Moreover, the four ellipsoids of the human embryo are only interesting as rudimentary organs, and they soon close up and disappear. The first three (between the first and second branchial arches) has any permanent significance ; from it are developed the tympanic cavity and the Eustachian tube. (Cf. Figs. 169, 326.)

It was Carl Gegenbaur again who solved the difficult problem of tracing the skeleton of the limbs of the Vertebrates to a common type. Few parts of the vertebrate body have undergone such infinitely varied modifications in regard to size, shape, and adaptation of structure as the limbs or appendages ; yet we are in a position to reduce them all to the same hereditary standard. We may generally distinguish three groups among the Vertebrates in respect to the formation of their limbs. The lowest and earliest Vertebrates, the Acoels and Cyclostomes, had, like their invertebrate ancestors, no pairs of limbs, as we see in the Anophtorans and the Ctenophores to-day (Figs. 320, 327). The second group is formed of the two classes of the two-finned and the Diplopoda ; here there are always two pairs of limbs, at first, in the stage of many-finned fish—two pair

of forelimbs or forelegs, and one pair of belly-fins or hind legs (Figs. 245–252). The third group comprises the four higher classes of Vertebrates—the Amphibia, Reptiles, Birds, and Mammals ; in these quadrupeds there are at first the same two pairs of limbs, but in the class of five-toed feet. Frequently 1 there five toes, and sometimes the first is wholly wanting (Fig. 253). But the original state-form of the group had five toes or fingers before and behind (Figs. 263–265).

The true primitive form of the pairs of appendages they were found in primitive fishes of the Silurian period, so preserved far up in the Atrypian deposit, the remarkable Conularia (Fig. 322). Both the hypaxial and the belly-fin are flat oval plates, in which we find a bimini cartilaginous skeleton (Fig. 256). This consists, firstly, of a much exaggerated fore- or "main" (A. B.), which runs through the fin from base to tip ; and secondly of a dorsal row of thin articulated semi-rings (r. r.), which are attached to both sides of the fin-rod. This is the skeleton of a feathered leaf. This primitive fin, which Gegenbaur first recognized, is attached to the vertebral column by a septum in the shape of a cartilaginous

It has probably originated from the tail.

material, probably

so more or less preserved in the fossilized remains of the earliest Sacellid (Fig. 320), Gnathides (Fig. 253), and Diplopoda (Fig. 254). It is also found in modified form in some of the actual sharks and rays, but in the majority of the Sacellid it has already degenerated to the extent that on each on one side of the fin-rod have been partly or entirely lost, and are retained only on the other (Fig. 257). Thus gets the universal fin, which has passed from the Sacellid to the rest of the fishes (Fig. 321).

Gegenbaur has shown how the first limb of the Amphibia, that just be-

<sup>1</sup> While Gegenbaur states

that they have been developed from a pair of originally webbed limbs of the fish,

the flesh of the four higher classes is enclosed at the same time in the skin, and passes along under cover in the epidermis, and only the fifth toe is now differently situated to that of the other dorsal or ventral, and not in the



FIG. 367.

FIG. 367.—Human skeleton, seen from behind.  
FIG. 368.—Structure of the clavicle. FIG. 369.



FIG. 368.

In the dorsal extensors of the Amphibia the multi-articular strength, and are lost, for the most part, on the other side of the dorsal, as well the lighter cartilages in Fig. 139b. Only the first lower vertebra (labeled in the illustration) are preserved; and these are the four lower vertebrae of the tail (first to fourth). The tail or caudal fin is developed from the lower end of the dorsal. From the middle and upper part of the flared caudal was developed the long spine of the tail—the important median caudal spine (Fig. 139c and d) and lamellae (Fig. 140) of the higher Vertebrates.

In this way the five-toed foot of the Amphibia, which we find even in the Cambrian *Sphaeropeltis* (Fig. 261), and which was inherited from them by the reptiles on one side and the mammals on the other, was formed by gradual degeneration and differentiation from the many-toed feet (Fig. 261). The reduction of the right six toes was accompanied by a further differentiation of the lateral. In mammals, segmentation was opposed from below, and the formation of the toes of the hind limb is composed principally of three broad digits and divided in the higher Vertebrates. The simple arch of the original amphibian digits was replaced by two upper (dorsal) pairs, the anterior (dorsal) / posterior, and a lower (ventral) pair. One anterior pair of the latter forms the primitive carpal (glenoid joint), and the posterior pair the metacarpal. In the same way the simple arch of the pelvic girdle became upper (dorsal) pairs, the ilio-femoral (or sacro), and a lower (ventral) pair. The anterior part of the latter forms the primitive sacroiliac (acetabulum), and the posterior the ischial bone (or ischi).

There is also a progressive separation between the fore and hind limb in the Mammals. The first section of the limb is supported by a single strong bone (the humerus in the fore, the femur in the hind limb). The second section consists of two bones: in front the radius (r.) and ulna (u.), behind the tibia and fibula. The differences in Figs. 262, 263, 264a, and 264b. The remaining numerous small bones of the wrist (carpal) and ankle (tarsal) are also similarly arranged in the fore and hind extremities, and so are the five bones of the middle-hand (metacarpal) and middle-foot (metatarsal). Finally, it is the same with the toe division, which

from a series of long plates below and behind. We find a complete parallel in all the parts of the fore leg and the hind leg.

When we then turn from comparative anatomy that the skeleton of the human limbs is composed of just the same bones, put together in the same way, as the skeleton in the four higher classes of Vertebrates, we may at once infer a common origin of them from a single monad. This monad was the earliest subdivision that had five toes on each foot. It is particularly the outer parts of the limb that have been modified by adaptation to different conditions. We need only recall the various ramifications they suffer when the mammal runs. We have the slender legs of the deer and the strong springing legs of the kangaroo, the climbing feet of the shrew and the digging feet of the mole, the fins of the whale and the wings of the bat. It will readily be grasped that these organs of locomotion differ as much in regard to size, shape, and special function as can be conceived. Nevertheless, the basic plan is substantially the same in every case. In the different limbs we always find the same structures, though in essentially the same rapidly changing connection. This is a splendid proof of the theory of evolution as regards a skeleton that can decrease in any organ of the body. It is true that the problem of the origin of the human forelimbs undergoes differentiation and degeneration before the spinal bifurcation (Fig. 264). Thus we find the first finger of the thumb developed on the fore-limb (or hand) of the dog (1). It has already disappeared in the hog (2) and eagle (3). In the next stage (such as the cow, 161) the second and fifth toes are also suppressed, and only the third and fourth are well developed (4). Nevertheless, all these different five-toed, as well as the hand of the ape (Fig. 360) and of man (Fig. 361), were originally developed from a common pentadactyl stem-form. This is proved by the rudiments of the degenerated toes, and by the similarity of the arrangement of the web-bones in all the pentadactyl (Fig. 362-365).

If we suddenly compare the bony skeleton of the human arm and hand with that of the lowest anthropoid apes, we find an almost perfect identity. This is especially true of the shoulder. In

parts, the lowest Eocene fauna of the *Valdésia* of Capo (Fig. 3a) are midway between the stromatoporoids (Fig. 3a) and the bivalves (Fig. 3a). There doubtless are the differences in structure and the proportions of the various parts between the different genera of each faunal group (Figs. 3a-3d); and still greater is the morphological diversity between them and the lower ones (the *Cryptostrophus*, *Hiatella*, *Spirifer*, *Leptena* and *Thyasites* faunas); therefore the difference of Shaler's *peritrochites* point (Fig. 3a).

The complete unity of structure which is thus exhibited by the comparative anatomy of the bone is fully confirmed by their histology. However different the epiphyses of the fine-toothed Cetaceans may be in their adult stage, they all develop from the same embryonic structure. In every case the first part of the shaft at the extremity - a very simple protuberance over the greater part of the side of the hypophysis. This simple protuberance develops directly into bone in the fishes and Ixodidae by differentiation of their cells. In the higher classes of Vertebrates each of the four plates takes the shape by no further growth of a head with a stalk the same half remaining horizontal and shorter and the other half broader and sharper. The upper half (the stalk of the head) then divides into two surfaces the upper and lower parts of the bone. All the eight longitudinal lobulations are formed at the free edge of the head, and gradually deeper, these are the creases between the toes (Fig. 134). The bone now makes three compartments. But at first all the toes, both of fore and hind feet are connected by a thin membrane like a webbing-work; they receive as of the original shaping of the foot as a padding. The further development of the bone from the rudimentary structure takes place in the same way in all the Vertebrates according to the laws of heredity.

The aetiological development of the sarcina, or active organs of infection, is not less interesting than that of the tubercle, or *latent* organs. But the comparative anatomy and embryology of the muscular system are much more difficult and laborious, and consequently have hitherto been but studied. We can therefore only draw some general physiognomical conclusions, therefore.

It is inconceivable that the administration of the Washington law has caused the

that of lower Crustaceans; and among them we have to consider especially the *orthopneustid* Vertebrates. They have a simple exoskeletal musculature kept dorsiflexing from the ventricle. This was afterwards replaced by a pair of branched heart muscles, this developed from the middle wall of the ventral pericardium; we still find the fine evidence of the muscle arising from the mesothelial side of these in the embryo of all the Vertebrates (cf. Figs. 124, 130-131, and 4 next). In the trachealized crustaceans of the *Lamellibranchia*, which we have studied the *Pectinibranchia*, the two endostrophes, and therefore also the chondro-phores of their walls, were not yet segmented. A great advance was made in the arthropods of these, as we have followed it step by step in the *Amygdaloidae* (Figs. 125, 130). The segmentation of the midline was the anterodorsal intersegmental process which very gradually, and the development of the ventralis stage, began. The articulation of the elements was after due segmentation of the muscular system, and the two paired lines very clearly delineated.

The epibiontic or dorsal system-muscles of the Anemone, Oculinaria, and Eudistoma (Fig. 363) first develop from local layers of muscle-wall (from the cell layer that lies directly on the ventral plate [ad] and the musculature [m.v.]) a lining myoepithelial (myo). By dorsal growth (d) it also reaches the external wall of the column-muscle, and presents there the dorsal to the ventral wall. From these segmental myoepithelia, which are clearly recognisable in the segmentation of the Verrucularia, proceed the lateral muscles of the anemone as we find in the amphipods in the Amphipoda (Fig. 364). By the formation of a "bulbous" ventral system there divide on each side a ventral upper and lower series of myoepithelia, dorsal and ventral lateral muscles. This is seen with typical regularity in the transverse section of the cell of a Polyp (Fig. 365). From these latter lateral muscles of the anemone develop the greater part of the subepidermic muscles of the trunk and also the "soft hair" muscular basis of the tentacles.

卷之三

## CHAPTER XXVII.

## THE EVOLUTION OF THE ALIMENTARY SYSTEM

The chief of the vegetal organs of the human frame, to the evolution of which we now turn our attention, is the alimentary canal. The gut is the oldest of all the organs of the metazoic body, and it leads us back to the earliest age of the formation of organs—in the first section of the Laurentian period. As we have already seen, the result of the first division of labour among the homogeneous cells of the earliest multicellular animal body was the formation of an alimentary cavity. The first duty and first need of every organism is self-preservation. This is met by the function of the nutrition and the covering of the body. When, therefore, in the primitive globular *Zooids* the homogeneous cells began to effect a division of labour, they had first to meet this twofold need. One half were converted into alimentary cells and formed a digestive cavity, the gut. The other half became covering cells, and formed an envelope round the alimentary tube and the whole body. Thus arose the primary gastral layers—the inner,

outer, covering, or animal layer. (Cf. pp. 814-17.)

When we try to construct an animal frame of the simplest conceivable type, that has some such primitive alimentary canal and the two primary layers constituting its wall, we inevitably come to the very remarkable embryonic form of the gastrula, which we have found with extraordinary persistence throughout the whole range of animals, with the exception of the unicellulars—in the Sponges, Cnidaria, Platydes, Vermilia, Molluscs, Articulates, Echinoderms, Trilobites, and Vertebrates. In all these stems the gastrula recurs in the same very simple form. It is certainly a remarkable fact that the gastrula is found in various animals as a larva-stage in their individual development, and that this gastrula, though much disguised by convergent

modifications, has everywhere essentially the same palaeontic structure (Fig. 30-32). The elaborate alimentary canal of the higher animals develops entirely from the same simple primitive gut of the gastrula.

The gastrula theory is now accepted by nearly all zoologists. It was first supported and partly modified by Professor Max-Liebermann, his pamphlet three years ago on his view on the development of the Mollusca, (1893) to give the name of *australophae* to the primitive gut and *Macrophae* to the primitive mouth.

Before we follow the development of the human alimentary canal in detail, it is necessary to say a word about the general features of its composition in the fully-developed man. The mature alimentary canal in man is constructed in all its main features like that of all the higher mammals, and particularly resembles that of the Cetaceans, the macro-mammals of the Old World. The animal into it, the oesophagus, is armed with thirty-two teeth, fixed in rows in the upper and

lower jaws. The cavity of the mouth is exactly the same as that of the Cetaceans, and differs from that of all other animals (p. 227). Above the mouth-cavity is the double nasal cavity; they are separated by the palate-wall. But we see that this separation is not there from the first, and that originally there is a common mouth-nasal cavity in the embryo; and this is only divided afterwards by the hard palate into two—the nasal cavity above and that of the mouth below (Fig. 342).

At the back the cavity of the mouth is half closed by the vertical curtain that we call the soft palate, in the middle of which is the uvula. A glances into a mirror with the mouth wide open will show its shape. The uvula is interesting because, besides man, it is only found in the ape. At each side of the soft palate are the tonsils. Through the curved opening that we find

underneath the soft palate we penetrate into the gullet or pharynx behind the mouth-cavity. Into this opens on either side a narrow canal (the *Hypopharyngeal tube*), through which there is direct communication with the tympanic cavity of the ear (Fig. 340 *c*). The pharynx is continued in a long, narrow tube, the *oesophagus* (*trachea*). By this the food passes into the stomach when masticated and swallowed. In the gut also opens, right above, the *trachea* (*trachea*), that leads to the lungs.

The cartilaginous epipharynx is found only in the mammals, and has developed from the fourth branchial arch of the fishes and amphibia. The lungs are found, in some and all the mammals, to the right and left in the pectoral cavity, with the heart between them. At the upper end of the trachea there is, under the epipharynx, a specially differentiated part, strengthened by a cartilaginous lappet, the *larynx*. This important organ of human speech also develops from a part of the alimentary canal. In front of the larynx is the thyroid gland, which now usually enlarges and forms goitre.

The oesophagus descends into the pectoral cavity along the ventral column, behind the lungs and the heart, pierces the diaphragm, and enters the ventral cavity. The diaphragm is a musculomuscular partition that completely separates the thoracic from the abdominal cavity in all the mammals (and these alone). This is evolutionarily not found in the beginning; there is at first a common breast-thoracic cavity, the *coeloma* or pleuro-peritoneal cavity. The diaphragm is formed later on as a muscular horizontal partition between the thoracic and abdominal cavities. It then completely separates the two cavities, and is only pierced by several organs that pass from one to the other. One of the chief of these organs is the oesophagus. After this has passed through the diaphragm, it expands into the *gastric sac* to which digestion takes place.

adult man (Fig. 340) is a long, somewhat expanding on the left into a sac of the stomach (*fundus*), and narrowing on the right, and passing at the *pylorus* (*stomach*) into the small intestine. At this point there is a valve, the *pyloric valve* (*valve pylori*), between the two sections of

the canal; it opens only when the pulpy food passes from the stomach into the intestine. In man and the higher Vertebrates the stomach itself is the chief organ of digestion, and is especially occupied with the selection of the food; this is not always so in many of the lower Vertebrates, which have no stomach, and discharge the faeces by a part of the gut further on. The muscular wall of the stomach is comparatively thick; it has externally strong muscles that accomplish the digestive movements and intestine.

glands, which secrete the gastric juice.

Next to the stomach comes the longer section of the alimentary canal, the *small gut* or *small intestine*. Its chief function is to absorb the peptised fluid



FIG. 340.—Diagram of stomach and duodenum, longitudinal section. *a*, oesophagus; *b*, fundus of stomach; *c*, hypopharynx; *d*, trachea; *e*, liver; *f*, gall-duct; *g*, duodenum; *h*, pancreas; *i*, head of the pancreas; *j*, tail of the pancreas. (From Gray.)

mass of food, or the chyle, and it is subdivided into several sections, of which the

(next to the stomach) is called the *duodenum* (Fig. 340 *g*/*h*). It is a short, horizontal-shaped loop of the gut. The *pancreatic* glands of the skin open into it—the liver, the chief digestive gland, that secretes the gall, and the pancreas, which secretes the pancreatic juice. The two glands pour their secretions, the bile and pancreatic juice, close together into the *stomach* (*fundus*). The opening of the gall-duct is of particular physiological importance, as it is the same in all the Vertebrates, and indicates the principal point of the hepatic or *trunk-gut* (Gastric-trunk). The liver, physiologically older than the stomach, is a large gland, rich in blood, in the adult man, immediately under the diaphragm on the left

side, and separated by it from the large. The pancreas lies a little further back and meets to the left. The remaining part of the small intestine is so long that it has to coil itself in many folds in order to find room in the narrow space of the abdominal cavity. It is divided into the jejunum above and the ileum below. In the last section of it is the part of the small intestine at which in the embryo the yolk-sac opens into the gut. This long and thin intestine then passes into the large intestine, from which it is cut off by a special valve. Immediately behind this "Basten-valve" the first part of the large intestine forms a wide, pouch-like structure, the cecum. The suspended end of the cecum is the famous rudimentary organ, the



FIG. 120.—Sagittal section of the head of a horse, showing the digestive tract, liver, gall-bladder, and pancreas. The dimensions of the corresponding parts in man are given in brackets.

vermiform appendix. The large intestine (*cæcum*) consists of three parts—an ascending part on the right, a transverse middle part, and a descending part on the left. The latter finally passes through an S-shaped bend into the last section of the alimentary canal, the rectum, which opens behind by the anus. Both the large and small intestines are supplied with numbers of small glands, which secrete mucus and other fluids.

For the greater part of its length the alimentary canal is attached to the inner dorsal surface of the abdominal cavity, or to the lower surface of the vertebral column. The fixing is accomplished by means of the thin suspensory plate that we call the mesentery.

Although the fully-formed alimentary canal is then a very elaborate organ, and this is due to its having a quantity of superfluous tissue, it has a quantity of simple structure.

The simplest structure has been naturally evolved from the very simple form of the primitive gut. We find in gnathostome-anectopore, and that every gnathostome brings before us to-day. We have already pointed out (Chapter IX.) how the oesophagus of the mammals (Fig. 67) can be reduced to the original type of the teleostean, which is now preserved by the amphioxus alone (Fig. 35). Like the latter, the human oesophagus and that of all other mammals must be regarded as the degenerate reproduction of the phylogenetic form that we call the gut-tube, in which the whole body is nothing but a double-walled gastric sac.

We already know from embryology the manner in which the gut develops in the embryo of man and the other mammals. First the gut-tube is first formed by a spherical end beyond which is filled with fluid (gastric juice, Fig. 105). In the dorsal end of this the polo-shaped entoderm shield is developed, and on the under-side of this a shallow groove appears in the middle line, the first trace of the fore, secondary alimentary tube. This groove becomes deeper and deeper, and its edges bend towards each other, and finally form a tube.

As we have seen, this single cylindrical gut-tube is at first completely closed before and behind in man and in the vertebrates generally (Fig. 105); the permanent openings of the alimentary canal, the mouth and anus, are only formed later on, and from the outer skin. A mouth-gut appears in the skin in front (Fig. 120 A), and this grows forwards the blind terminal of the cavity of the hind-gut (Fig.), and at length reaches thus to the nose; at a shallow anastomosis is formed in the skin behind, which grows deeper and deeper, advances towards the blind blind end of the pelvic gut, and at last connects with it. There is at first both before and behind, a thin partition between the exterior coelomous pit and the blind end of the gut—the thoraco-coelom in front and the peritoneal cavity behind; these disappear when the connection takes place.

Directly in front of the anus-opening the alimentary develops from the blind gut; this is the important embryonic structure

that forms into the placenta, in the Placentalia (including man). In this more advanced form the human alimentary canal (and that of all the other mammals) is a slightly bent, cylindrical tube, with an opening at each end, and two appendages growing from its lower wall: the anterior one is the umbilical vesicle or yolk-sac, and the posterior the allantois or urinary sac (Fig. 151).

The thin wall of this simple alimentary tube and its ventral appendages is, save on microscopic examination, composed of two strata of cells. The inner stratum, lining the entire cavity, consists of larger and darker cells, and is the gut-gland layer. The outer stratum consists of smaller and lighter cells, and is the gut-fibre layer. The only exception is in the cavities of the mouth and anus, because those originate from the side. The inner part of the mouth-cavity is not provided by the gut-gland layer, but by the skin-tissue layer; and its muscular development is provided, not by the gut-fibre, but the skin-fibre layer. It is the same with the wall of the anal sac-cavity.

If it is asked how those continuous layers of the primitive gut-wall are related to the various tissues and organs that we find afterwards in the fully-developed system, the answer is very simple. It can be put in a single sentence. The epithelium of the gut—that is to say, the internal soft stratum of cells that lines the cavity of the alimentary canal and all its appendages, and so immediately occupied with the processes of nutrition—is formed solely from the gut-gland layer, all other tissue and organs that belong to the alimentary canal and its appendages originate from the gut-fibre layer. From the latter is also developed the whole of the outer envelope of the gut and its appendages; the fibrous connective tissue and the smooth muscles that compose its muscular layer, the cartilages that support it (such as the cartilages of the larynx and the trachea), the blood-vessels and lymph-vessels that absorb the nutritive fluid from the intestine—in a word, all that there is to the alimentary system besides the epithelium of the gut. From the same layer we also get the whole of the mesentery, with all the organs included in it—the heart, the large blood-vessels of the body, etc.

Let us now leave this original structure of the mammal gut for a moment, in

order to compare it with the alimentary canal of the lower Vertebrates, and of those Invertebrates that we have recognized as man's ancestors. We find, first of all, in the lowest Metazoa, the Coelomaria, that the gut remains permanently in the very simple form in which we find it (translatingly in the palingenetic gut-tube of the other animals); it is then in the Gastrozoaria (*Proctostomes*), the Polyparia (*Prophytomes*), the simplest Sponges (*Oicyathidae*), the freshwater Polyps (*Bryozoa*), and the ascidio-embryos among other Cestatoria (Fig.



FIG. 152.—Section of Malpighian tubules of a planarian (Gastrotrich). A longitudinal section, showing the arrangement of the Malpighian tubules throughout the body. (From Cope.)

152). Even in the simplest forms of the Planaria, the Rhombocoela (Fig. 150), the gut is still a simple straight tube, lined with the entoderm; but with the important difference that in this case its single opening, the primitive mouth (m.), has forced a muscular gullet (ad.) by invagination of the skin.

We have the same simple form in the gut of the lowest Vermalia (Gastrotricha, Fig. 242, Nemertines, Nematodes, etc.). But in these a second important opening of the gut has been formed at the opposite end to the mouth, the anus (Fig. 153 a).

We see a great advance in the structure of the vertebrate gut in the remarkable *Bivalvephores* (Fig. 213), the sole survivor of the Entoproctina class. Here we have the first appearance of the division of the alimentary tube into two sections that characterizes the Chordata. The fore part, the head-gut (*foregut*), becomes the organ of respiration (branchial gut, Fig. 213 A); the hind part, the trunk-gut (*metagut*), alone acts as digestive organ (hepatic gut, 2).

respiratory branchial gut, the posterior the digestive hepatic gut. In both it develops polypogenetically from the primitive gut of the gastrula, and in both the hinder end of the medullary tube covers the primitive mouth to such an extent that the remarkable medullary intestinal duct is formed, the passing communication between the neural and intestinal tubes (*coelomic oesophagus*, Figs. 82, 85 &c.). In the vicinity of the closed primitive mouth, possibly in its place, the fore

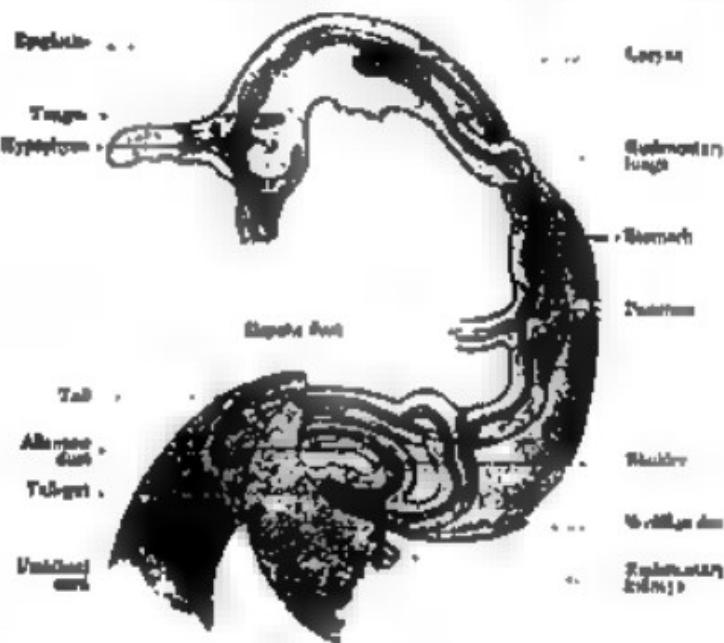


FIG. 213.—One of a bivalve embryo, consisting of an anterior, respiratory, hepatic part, and a posterior, digestive, hepatic part. (From J. H. V.)

The differentiation of these two parts of the gut in the Enteropneusts is just the same in all the Taxa.

It is particularly interesting and instructive in this connection to compare the Enteropneusts with the Ascidiidae and the Amphioxus (Figs. 220, 221)—the remarkable animals that form the connecting link between the Invertebrates and the Vertebrates. In both forms the gut is of substantially the same construction; the anterior section forms the

mouth is developed. In the same way the mouth is a fresh formation in the Amphioxus and the Ascidia.

and that the Ctenophores generally. The secondary formation of the mouth in the Chordonia is probably connected with the development of the gill-slits which are formed in the gut-wall immediately behind the mouth. In this way the anterior section of the gut is converted into a respiratory organ. I have already pointed out that this modification is distinctive of the

Vertebrates and Tunicates. The phylogenetic appearance of the gill-clefts indicates the commencement of a new epoch in the stem-history of the Vertebrates.

In the further ontogenetic development of the alimentary canal in the human embryo the appearance of the gill-clefts is the most important process. At a very early stage the gut-wall joins with the external body-wall in the head of the human embryo, and this is followed by the formation of four clefts, which lead directly into the gut from without, on the right and left sides of the neck, behind the mouth. These are the gill or guttural clefts, and the partitions that separate them are the gill- or guttural arches (Fig. 171). These are most interesting embryonic structures. They show us that all the higher Vertebrates reproduce in their earlier stages, in harmony with the biogenetic law, the process that had so important a part in the rise of the whole Chordata. This process was the differentiation of the gut into two sections—an anterior respiratory section, the branchial gut, that was restricted to breathing, and a posterior digestive section, the hepatic gut. As we find the highly characteristic differentiation of the gut into two different sections in all the Vertebrates and all the Tunicates, we may conclude that it was also found in their common ancestors, the Proctonotaria—especially as even the Echinoderms have it. (Cf. pp. 119, 151, 227, and Figs. 210, 220, 245.) It is entirely wanting in all the other Invertebrates.

There is at first only one pair of gill-clefts. In the Amphioxus, as in the Acanthini and Enteropneusts, and the Cyclopoids (Fig. 245) there is only one pair throughout life. But the number progressively increases in the former. In the Craniota, however, it decreases still further. The Cyclostomes have six to eight pairs (Fig. 247); some of the Selachii six or seven pairs, most of the fishes only four or five pairs. In the embryos of man, and the higher Vertebrates generally, when they make an appearance at an early stage, only three or four pairs are developed. In the fishes they remain throughout life, and form an exit for the water taken in at the mouth (Figs. 248, 249). But they are partly lost in the amphibia, and entirely in the higher Vertebrates. In these nothing but a cleft of the first gill-cleft. This is

transformed into a part of the organ of hearing; hence it has developed the external meatus, the tympanic cavity, and the Eustachian tube. We have already considered these remarkable structures, and need only point here to the interesting fact that our middle and external ear is a modified inheritance from the fishes. The branchial arches also, which separate the clefts, develop into very different parts. In the fishes they remain gill-arches, supporting the respiratory gill-blades. It is the same in the lower amphibia, but in the higher amphibia they undergo various



Fig. 220.

Fig. 221.

FIG. 220.—*Long. sec. of a dog-embryo (12 days = Fig. 219) from Nansen's Ann. from the ventral side. A diagram shows the relations of pharynx and larynx, a large oesophagus, & a large bulk of the liver situated in front, while the middle gut opens with a wide aperture.*

FIG. 221.—*The same dog-embryo from the right, showing stomach, liver, & intestine, & mesentery, & mesone.*

modifications, and in the three higher classes of Vertebrates (including man) the hyoid bone and the osseous of the ear develop from them. (Ex. p. 291.)

From the first gill-arch, from the outer surface of which the muscular tongue processes, we get the first structure of the mandibular skeleton—the upper and lower jaws, which surround the mouth and support the teeth. These important parts are wholly wanting in the two lowest classes of Vertebrates, the Acrania and Cyclostomes. They appear first in the earliest Selachii (Figs. 248-251), and have been transmitted from this stem-group of the Gnathostomes to the higher

Vertebrates. Hence the original formation of the skeleton of the mouth can be traced to these primitive fishes, from which we have inherited it. The teeth are developed from the skin that clothes

it encloses the gut of the earliest Vertebrates (Cephalochorda). It then divides into two sections, a fore or branchial gut and a hind or hepatic gut, like the of the Branchiostomes, the Ascidia, and the Amphioxus. The formation of the jaws and the branchial arches changes it into a real sub-gut (*subgaster*). But the branchial gut, the one reminiscence of our fish-ancestors, is afterwards atrophied as such. The parts of it that remain are converted into entirely different structures.

But, although the anterior section of our alimentary canal thus inherits from its original character of branchial gut, it retains the physiological character of respiratory gut. We are now astonished to find that the permanent respiratory organ of the higher Vertebrates, the air-breathing lung, is developed from this first part of the alimentary canal. Our lungs, trachea, and larynx are formed from the ventral wall of the branchial gut. The mouth of the respiratory apparatus, which occupies the greater part of the pectoral cavity in the adult man, had first merely a small pair of vesicles or bladders, which grew out of the floor of the buccal

FIG. 350.—Transverse section of the head of a *Pisces* (Teleostei). A longitudinal groove above it is the mouth groove; the upper jaw is shown in white, a muscle of the mouth, a lateral view of the teeth.

the jaws. As the whole mouth cavity originates from the outer integument (Fig. 350), the teeth also must come from it. As a fact, this is found to be the case on microscopic examination of the development and finer structure of the teeth. The scales of the fishes, especially of the shark type (Fig. 351), are in the same position as their teeth in this respect (Fig. 352). The dentine matrix of the teeth (dentine) develops from the epidermis; its enamel covering is a secretion of the epidermis that covers the enamel. It is the same with the cutaneous teeth or placoid scales of the Selachii. At first the whole of the mouth was armed with these cutaneous teeth in the Selachii and in the earliest amphibia. Afterwards the formation of them was restricted to the edges of the jaws.

Hence our human teeth are, in relation to their original source, modified placoid scales. For the same reason we must regard the salivary glands, which open into the mouth, as epidermic glands, as they are formed, not from the glandular layer of the gut like the rest of the alimentary glands, but from the epidermis, from the horny plate of the outer peritoneal layer. Naturally, in connexion with this evolution of the mouth, the salivary glands belong genetically to one series with the sudoriferous, sebaceous, and mammary glands.

Thus the human alimentary canal is as simple as the primitive gut of the *gnatharia* in its original structure. Later



FIG. 352.—Transverse sections of the head of a *Pisces* (Teleostei). From Copepod. In section A the pharynx (A) is seen. See the hypopharyngeal groove, groove of the mouth, and mouth. A, B, C, D, E, F, G, H.

and immediately behind the gills (Figs. 353, 357, 447, 45). These vesicles are found in all the Vertebrates except the two lowest classes, the Agnatha and Cyclostomes. In the lower Vertebrates they do not develop

ups, but into a large air-bladder, which occupies a good part of the body-cavity and has a wide dorsal port. It serves, not for breathing, but to effect swimming movements up and down, and so is a sort of hydrostatic apparatus—the floating bladder of fishes (*Auctoritas*, p. 233). However, the human lungs, and those of all air-breathing Vertebrates, develop from the same simple vesicular appendage of the head-gut that becomes the floating bladder in the fishes.

At first this bladder has no respiratory function, but merely acts as hydrostatic apparatus for the purpose of increasing or lessening the specific gravity of the body. The fishes, which have a fully-developed floating bladder, can force it together, and thus condense the air in it. This air also escapes whistling from the alimentary canal, through an air-duct that connects the floating bladder with the pharynx, and is ejected by the mouth. This lessens the size of the bladder, and so the fish becomes heavier and sinks. When it wishes to rise again, the bladder is expanded by releasing the pressure. In many of the Cetaceans the wall of the bladder is covered with myo-fibrils in the Trinucleic Unions (Fig. 254).

This hydrostatic apparatus begins the Diaphragm to change into a respiratory organ; the blood-vessels in the bladder now do longer move

all themselves, but also take air through the surface. This process reaches its full development in the Amphibia. In them the floating bladder is turned into lungs, and the air-passages into a trachea. The lungs of the Amphibia have been transmitted to the three higher classes of Vertebrates. In the lower Amphibia the lungs on either side are still very simple transversal sacs with thin walls, as in the common salamander, the Triton. It still certainly resembles the floating bladder of the fishes. It is true that the Amphibia have no lungs, right and left. But the floating bladder is also double in many of the fishes (such as the eel, Gasterosteus), and divides into right and left halves. On the other hand, the lung is single in Ceratodus (Fig. 257).

In the human embryo and that of all the other Acanthostomes the lungs develop from the blind part of the ventral wall of the head-gut (Fig. 258). Immediately behind the single structure of the thyroid

gland a vascular groove, the rudiment of the trachea, is detached from the gut. From its hinder end a couple of vesicles develop—the simple tubular rudiments of the right and left lungs. They afterwards increase considerably in size, so the greater part of the thoracic cavity, and take the heart between them.

As we find in the frog we find that the simple sac has developed into a spongy body of peculiar trache-like tissue. The originally short connection of the pulmonary sac with the head-gut extends into a long, thin tube. This is the wind-pipe (trachea); it opens into the gut above, and divides below into two branches which go to the two lungs. In the wall of the trachea



FIG. 258.—Diagram and photograph of a human embryo of twelve weeks, natural size. The trachea is the head of a serpent. Virtually and perfectly well developed. The greater part of the body is filled with a sacrum with the liver, from the middle part of which the oesophagus and the ventricle receive the peritoneum. Above the diaphragm, on the ventral side of the heart, to the right and left of it are the two small lungs.

circular cartilages develop, and these lungs expand. At its upper end, surrounded by pharyngeal opening, the larynx is formed—the organ of voice and speech. The larynx is found at various stages of development in the Amphibia, and consequently man is in a position to trace the progressive growth of this persistent organ from the rudimentary structure of the lower Amphibia up to the elaborate and delicate vocal apparatus of the larynx.

Refer here to an interesting rudimentary organ of the respiratory gut, the thyroïd gland, the large gland in front of the larynx, that has given the "Adam's

gut," and is often especially developed in the mole rats. It has a certain function, but yet fully understood—in the absorption of the body and arises in the mouth or somewhere from the lower part of the pharynx. In many young dentrites the thyroid gland is partially fused in dorsal development, and then from either a growth that hangs in the front of the neck, but it is much more interesting phylogenetically. An attempt is often made, however, to show this evolutionary stage in the low molls of the hydromedusae considered in a previous chapter, and such was at the middle of the pharynx in the Anthozoa and Ctenophora, and comes back to the present. Cf. p. the Fig. 100. We find it in the original situation in the head of the Cyclostomes (Fig. 100 and 294).

The second section of the alimentary canal, the mouth or buccal, gut, undergoes no less important modifications during our vertebrate evolution than the first section. In tracing the further development of this digestive part of the gut, we find that most complex and elaborate organs originate from a very rudimentary original structure. For instance we may take the digestive gut (the fore gut) in the frog gut (trachea and oesophagus), the middle gut (duodenum, aorta, liver, gall-bladder, pancreas, and stomach), and the hind gut (colon and rectum). Here again we find certain given or approximations of the originally simple gut developing into a series of organs. Two of these anterior structures, the oesophagus and stomach, are already found in us. The is a large gland that opens into the duodenum, the liver and pancreas, are given off from the middle and third important part of the midgut.

Immediately behind the vestibular pullus of the lungs comes the origin of the alimentary canal that forms the oesophagus (Fig. 101) cf. Fig. 29. This is a simple organ, which is easily recognizable in the anterior end digestion of the food. It is not in the lower Vertebrates the great physiologically important and the simpler character that it has in the higher. In the Anthozoa and Ctenophora the anterior tube is not entirely closed; a real oesophagus is represented only by the duct that from the brain leads to the hypophysis gut. In some of the other tubes like the oesophagus is only a very simple partly closed tube, and at the beginning of the digestive canal,

of the gut, running straight from front to back in the median plane of the body, underneath the ventral aorta. In the mammals the first structure is just as rudimentary as it is fundamentally in the preceding. But its various parts begin to develop. As the left side of the spine-shaped sac grows much more quickly than the right, and as it runs obliquely to the left at the spine, it grows more to the right. The spine itself is more to the left, and the lower and more to the right. The foregut and hindgut are now the longer and narrower part of the mesogastrium. Underneath this on the left is the short one (mesentery of the oesophagus) (Fig. 102), and then the liver (cf. p. 294), and then the stomach (Fig. 103, Appendix 4). The original ring-shaped midgut elongates, running later to the left and owing to the right, and upper midgut and posterior to it. It reaches the posterior to the upper layer of the ventricle in all the mammals examined that developed a foregut and sacculus opening from the gullet-like lumen. In the older layer a number of small glandular tubules are formed from the gut-lumen, that secrete the gastric juice. At the lower end of the sacculus is developed the valve that separates it from the duodenum (Fig. 104, Fig. 300 d).

Underneath the stomach there now develops the disproportionately long mesentery of the small intestine. The development of this section is very simple, and consists essentially in an extremely rapid and considerable growth lengthways. It is at first very short, quite straight, and simple. But immediately behind the stomach we find at an early stage a bifurcating broad mid-gut of the gut, in connection with the appearance of the alimentary canal from the pharynx and the development of the fore-gastroscopy. The thin folds are continuing along beneath this lumen to the upper side of the ventral aorta, and with the development of the intestine however, in the fore-mesentery of the oesophagus (Fig. 105). We find at an early stage a considerable growth of the small intestine; it is then forced to roll itself in a number of loops. The various sections that are here to distinguish in it are differentiated in a very simple way—the descending part to the stomach, the ascending part, and the last section of the small intestine, the ileum.

From the duodenum are developed the two large glands that we have already mentioned—the liver and pancreas. The liver appears first in the shape of two small buds, that are found in the right and left immediately behind the stomach (Figs. 213, 5, 224, 2). In many of the lower Vertebrates they remain separate for a long time (in the Myxine they are still separate or are only imperfectly joined). In the higher Vertebrates they soon blend more or less completely to form a single large organ. The growth of the liver is very great at first. In the larvae embryo it grows so much in the second month of development that in the adult it occupies by far the greater part of the body-cavity (Fig. 267). As then the two buds develop equally, afterwards the left fails to hinder the right. In consequence of the unopposed development and turning of the stomach and other abdominal viscera, the whole liver is now pushed to the right side. Although the liver does not always grow so disproportionately, it is considerably larger in the embryo than in the adult. Its weight relatively to that of the whole body is 1 : 36 in the adult, and 1 : 18 in the embryo. Hence it is very important physiologically during embryonic life, it is chiefly concerned in the formation of blood, but as much in the excretion of nitrogen.

Immediately behind the liver a second large paired gland develops from the duodenum. One posterior or pancreatic. It is wanting in most of the lower classes of Vertebrates, and is then found in the fishes. This organ is also an evagination from the gut.

The last portion of the alimentary canal, the large intestine, is at first in the embryo a very simple, short, and straight tube, which opens behind the rectum. It receives that evagination that is the lower Vertebrates. But it grows considerably in the myxine, and into various folds, and divides into two portions, the first and longer of which is the cecum, and the shorter the rectum. At the beginning of the cecum there is a valve ("valve ileocecal") that separates it from the small intestine. Immediately behind this there is a second growth, which enlarges into the sacculus (Fig. 227, 2). In the placental mammals this is very large, but it

is very small in completely viviparous mammals. In man, and most of the apes, only the first portion of the cecum is wide; the blind end-part of it is very narrow, and seems largely to be merely a sacculus-appendage of the former. This "cecum-appendage" is very important as a rudimentary organ. The only significance of it in man is that not infrequently a cecum-sacculus or even older hard and indigestible matter penetrating into its narrow cavity, and by exciting inflammation and suppuration causes the death of otherwise sound skin. Pathology has great difficulty in giving a medical explanation of, and attributing to a function, this dreadful appendicitis. In our placental mammals this rudimentary organ was much larger and had a useful function.

Finally, we have important appendages of the alimentary tube in the bladder and rectum, which belong to the alimentary system. These urinary organs, acting as reservoirs and ducts for the urine excreted by the kidneys, originate from the lowermost part of the alimentary tract. In the Urodeles and Amphisbaenidae, in which the allantoic sac first makes its appearance, it remains within the body-cavity, and functions entirely as bladder. But in all the Aves and Mammals it grows far outside of the body-cavity, and forms the large "urogenital" ("prostate") bladder, from which the placenta develops in the higher mammals. This is lost at birth, but the long stalk or pedicle of the allantoic evagination, and those with its upper part the middle vesico-urethral ligament, a rudimentary organ that grows in the shape of a solid string from the vertex of the bladder to the rectal. The lowest part of the allantoic pedicle (or the "urachus") remains hollow, and forms the bladder. At first this opens into the last section of the gut to come in the lower Vertebrates. Then there is a valvular closure, which cuts off both rectum and sacculus. But among the mammals this closure is only permanent in the Monotremes, as it is in all the birds, reptiles, and amphibia. In all the other mammals (marsupials and placental) a transverse partition is also formed, and this separates the urino-genital organs in front from the rectum behind. (See p. 229 and Chapter XXIX.)

## CHAPTER XXVIII.

## EVOLUTION OF THE VASCULAR SYSTEM

Two uses that we have hitherto made of our biogenetic law will give the reader an idea how far we may trust its guidance in phylogenetic investigation. This differs considerably in the vascular systems of organs; the reason is that heredity and variability have a very different range in these systems. While some of them faithfully preserve the original paleozoic development inherited from earlier animal ancestors, others show signs trace of this rigid heredity; they are rather disposed to follow new and divergent course of development in consequence of adaptation. The organs of the first kind represent the conservative element in the multicellular state of the human frame, while the latter represent the progressive element. The course of histone development is a result of the correlation of the two tendencies, and they must be carefully distinguished.

There is perhaps no other system of organs in the human body in which this is more necessary than in that of which we are now going to consider the oblique development—the vascular system, or apparatus of circulation. If we were to draw our conclusions as to the original features in our earlier animal ancestors solely from the phenomena of the development of this system in the embryo of man and the other higher Vertebrates, we should be wholly misled. By a series of important embryonic adaptations, the chief of which is the formation of an extensive food-yolk, the original course of the development of the vascular system has been so much falsified and controlled in higher Vertebrates that

nothing now remains in their embryology of some of the principal phylogenetic features. We should be quite unable to explain these if comparative anatomy and embryology did not come to our assistance.

as and all the appendages of

cavities filled with juice or cell-containing fluid. These "vessels" (vascula) play an important part in the nutrition of the body. They partly conduct the nutritive and blood to the various parts of the body (blood-vessels); partly absorb from the gut the white chyle formed in digestion (lymph-vessels); and partly collect the used-up juices and convey them away from the tissues (lymphatic vessels). With the latter are connected the large cavities of the body, especially the body-cavity, or coeloma. The lymphatic vessels conduct both the colourless lymph and the white chyle into the venous part of the circulation. The lymphatic glands act as producers of new blood-cells, and with them is associated the spleen. The course of movement for the circulation of the fluids is the heart, a strong muscular sac, which contracts regularly and is equipped with valves like a pump. This constant and steady circulation of the blood vessels permits the complex metabolism of the higher animals.

But, however important the vascular system may be to the more advanced and larger and highly-differentiated animals, it is not at all so indispensable an element of animal life as is commonly supposed. The older science of medicine regarded the blood as the real source of life. Even in the still prevalent confused notions of heredity the blood plays the chief part. People speak generally of full blood, half blood, etc., and imagine that the hereditary transmission of certain characters "lies in the blood." The incorrectness of these ideas is clearly seen from the fact that in the act of generation the blood of the parents is not directly transmitted to the offspring, nor does the embryo possess blood in its early stages. We have already seen that not only the differentiation of the four secondary germinal layers, but also the first structures of the principal organs in the embryo of all the Vertebrates, take place long before there is any

trace of the vascular system—the heart and the blood. In accordance with this ontogenetic fact, we must regard the vascular system as one of the *latest* organs from the phylogenetic point of view, just as we have found the alimentary canal to be one of the *earliest*.

There is much later than the alimentary.

The important nutritive fluid that circulates as blood and lymph in the elaborate canals of our vascular system is not a clear, simple fluid, but a very complex chemical juice with millions of

The red colour of the blood is caused by the great accumulation of the former, the others circulate among them *silently*. When the *erythrocytes* increase at the expense of the white corpuscles, it is (for chloroform).

The lymphocytes (*leucocytes*), commonly called the "white corpuscles" of the blood, are phylogenetically older and more widely distributed in the animal world than the red. The great majority of the *Invertebrates* that have acquired an independent vascular system have only colourless lymphocytes in the circulation.



Fig. 348.



Fig. 349.

Fig. 348.—Red blood-cells of various mammals usually irregular; *a* of man; *b* cattle; *c* deer; *d* porpoise; *e* whale; *f* dog; *g* monkey (from *Nagel*); *h* lymphocytes (showing with a surface mark, *i*, indigo-carmine, (from *Hoyer*)).

A lymphatic duct the *anterior*—*posterior*

cells floating in it. These blood-cells are just as important in the complicated life of the higher animal body as the circulation of money is to the commerce of a civilized community. Just as the citizens meet their needs most conveniently by means of a financial circulation, so the various tissue-cells, the microscopic citizens of the multicellular human body, have their food conveyed to them best by the circulating cells in the blood. These blood cells (*haemocytes*) are of two kinds in man and all the other *Chordates*—red cells (*erythrocytes* or *erythrocites*) and colourless or lymph cells (*leucocytes*).

fluid. There is no exception in the *Monotremes* (Fig. 356) and some groups of *Amphibia*. When we examine the colourless blood of a ray-fish or a shark (Fig. 358) under a high power of the microscope, we find in each drop numbers of mobile leucocytes, which behave just like independent *Acanthæ* (Fig. 27). Like these unicellular *Protoplasts*, the colourless blood-cells creep slowly about, their usually plasma-body constantly changing its form, and stretching out finger-like processes set in one direction, then another. Like the *Acanthæ*, they take particles into their cell-body. On account

of this feature these ameboid phagocytes are called "eating cells" (phagocytes), and on account of their motions "wandering cells" (leucocytes). It has been shown by the discoveries of the last few decades that these leucocytes are of the greatest physiological and pathological consequence to the organism. They can absorb either solid or dissolved particles from the wall of the gut, and carry them to the blood in the chyle; they can absorb and remove undesirable matter from the tissues. When they pass in large quantities through the fine pores of the capillaries and accumulate at isolated spots, they cause inflammation. They can consume and destroy bacteria, the threatened vehicles of infectious disease; but they can also transport these micro-organisms, to fresh regions, and so extend the sphere

*glossy*) are irregularly distributed in the pores of their protoplasm. The red cells of most of the Vertebrates are elliptical flat disks, and enclose a nucleus of the same shape; they differ a good deal in size (Fig. 102). The mammals are distinguished from the other Vertebrates by the circular form of their biconcave red cells and by the absence of a nucleus (Fig. 1); only a few genera still have the elliptic form inherited from the reptiles (Fig. 2). In the embryo of the mammals the red cells have a nucleus and the power of increasing by cleavage (Fig. 103).

The origin of the blood-cells and vessels in the embryo, and their relation to the germline tissues and tissues, are among the most difficult problems of embryology—these obscure questions on which the most divergent opinions are still unchanged.



FIG. 10.—Transect across the front of a dune-slope. Surveyors staves old. (From Sauer [1936] *Geological Survey of Canada Memoir 120*, p. 12, with permission of the Canadian Government.) The dune-line is indicated by a line of trees, with a layer of pebbles across the slope.

of infection. It is probable that the sensitive and travelling leucocytes of the invertebrate animals have a powerfully co-operated for millions of years in the phylogenesis of the advancing animal organisations.

The red blood-cells have a much more restricted sphere of distribution and activity. But they also are very important in connection with certain functions of the craniote-organism, especially the exchange of gases or respiration. The cells of the dark red, carbonised or venous, blood, which have absorbed carbonic acid from the animal tissues, give this off in the respiratory organs; they receive instead of it fresh oxygen, and thus bring about the bright red colour that distinguishes oxydised or arterial blood. The red colouring matter of the blood (haemoglobin) is contained in the red blood-cells.

by the most competent scientists. In general, it is certain that the greater part of the cells that compose the vessels and their contents come from the mesoderm—in fact, from the guillotine layer; it was on this account that Baer gave the name of "vascular layer" to this visceral layer of the embryo. But other important observers say that a part of these cells comes from other germinal layers, especially from the pit-gland-layer. It seems to be true that blood-cells may be formed from the cells of the entoderm before the development of the mesoderm. If we examine sections of chicken, the earliest and most familiar subjects of embryology, we find at an early stage the "primitive arteries" we have already described (Fig. 56-*a*) in the ventral angle between the oesophagus (*Po*) and heart muscle (*H*). The

thin wall of these first vessels of the amniote embryo consists of flat cells (*endotheliose* or *vascular epithelia*); the fluid within already contains numbers of red blood-cells; both have been developed from the gut-layer layer. It is the same with the vessels of the germinative area (Fig. 368 c), which lie on the ectodermic membrane of the yolk-sac (c). These failures are seen still more clearly in the transverse section of the duck-embryo in Fig. 152 (p. 141). In this we see clearly how a number of stellate cells proceed from the "vascular layer" and extend in all directions in the "primary body-cavity" — i.e., in the spaces between the germinative layers. A part of these travelling cells come together and line the wall of the larger spaces, and thus form the first vessels, others enter into the cavity, live in the fluid that fills it, and multiply by cleavage—the first blood-cells.

But, besides these mesoectodermic cells of the "vascular layer" proper, other travelling cells, of which the origin and purpose are still obscure, take part in the formation of blood in the metazoite. Vertebrates (especially fishes). The chief of these are those that Rudolf has most aptly designated "macrocysts." These "swelling yolk-cells" are found in large numbers in the foot-synthet of the Salpæ, especially in the foot-wall—the border zone of the terminal disk in which the embryonic vascular net is first developed. The nuclei of the macrocytes become ten times as large as the ordinary cell-nuclei, and are distinguished by their strong capacity for taking colour, or their special richness in chromatin. Their protoplasmic body resembles the stellate cells of certain tissues (astrocytes), and behaves just like a rhizopod (such as Grönau); it sends out numbers of stellate processes all round, which ramify and stretch into the surrounding foot-silk. These variable and very mobile processes, the pseudopodia of the macrocyte, serve both for locomotion and for getting food; as in the real rhizopoda, they surround the solid particles of food (granules and plates of yolk), and accumulate round their nucleus the food they have received and digested. Hence we may regard them both as eating-cells

(phagocytes) and travelling-cells (plasmocytes). Their lively nucleus divides quickly and often repeatedly, so that a number of new nuclei are formed in a short time; as each fresh nucleus surrounds itself with a mantle of protoplasm, it provides a new cell for the construction of the embryo. Their origin is still much disputed.

Half of the twelve stems of the animal would have no blood-vessels. They make their first appearance in the Vermalia. Their earliest source is the primary body-cavity, the sanguiferous space between the two primary germinal layers, which is either a relic of the segmentation-mass, or is a subsequent formation. Amorphous proto-



FIG. 368.—Development of a blood-vessel in a Ctenophore larva. The figure shows a cross-section of the body wall with several small, circular blood vessels. One prominent vessel is shown in longitudinal view, revealing its internal structure with a central lumen and a thick wall. The surrounding tissue is labeled with various anatomical terms like 'epidermis', 'mesoglea', 'endoderm', 'gastrovascular system', 'mesogleal spaces', and 'mesogleal filaments'. The overall structure is elongated and somewhat transparent, showing internal cellular details.

cytes, which migrate from the mesoglea and reach this fluid-filled primary cavity, live and multiply there, and form the first collective blood-cells. We find the vascular system in this very simply formed in the Bryozoa, Rotifera, Nemertea, and other lower Vermalia.

The first step in the improvement of this primitive vascular system is the formation of larger canals or blood-conducting tubes. The spaces filled with blood, the veins of the primary body-cavity, receive a special wall. "Blood-vessels" of this kind (in the narrower sense) are found among the higher worms in various forms, sometimes very simple, at other times very complex. The first

that was probably the incipient structure of the elaborated vascular system of the Vertebrates (and of the Articulates) is found in two primordial principal vessels—a dorsal vessel in the middle line of the dorsal wall of the gut, and a ventral vessel that

#### MIDDLE LINE OF A ANNELID

dorsal vessel is evoked the aorta (or principal artery), from the ventral vessel the principal or subintestinal vein. The two vessels are connected in front and behind by a loop that runs round the gut. The blood contained in the two tubes is propelled by their peristaltic contractions.

The earliest Vermatines in which we find this primitive independent vascular system—the Nematomes (Fig. 244). As a rule, they have three parallel longitudinal vessels connected by loops, a single dorsal vessel above the

gut, and two—right and left.

In the Nemertines the blood is already coloured, and the red colouring matter is red haemoglobin, constituted with elliptical discoid cells, as in the Vertebrates. The further evolution of this rudimentary vascular system can be gathered from the class of the Annelids in which

we find it at various stages of development. First, a number of transverse connections are formed between the dorsal and ventral vessels, which pass round the gut ring-wise (Fig. 245). Other vessels grow into the body-wall and ramify in order to convey blood to it. In addition to the two large vessels of the middle plane there are often two lateral vessels, one to the right and one to the left; as, for instance, in the leech. There are four of these parallel longitudinal vessels in the Enteropneusts / Balanophores, Fig. 245). In these imperfect Vermatines the foremost section of the gut

has already been converted into a gill-crate, and the vascular arches that rise in the wall of this the dorsal vessel has become branched vessels.

We have a further important advance in the Thaliaceans, which we have recognized as the ancestral blood-relatives of our early vertebrates, and

the heart—i.e., a central organ of circulation, driving the blood *out* the vessels by the regular contractions of its muscular wall. It is of a very rudimentary character, a spindle-shaped tube, passing at both ends into a principal vessel (Fig. 251). By its original position behind the gills

(sometimes in, sometimes less, forward), the heart we clearly that it has been formed by local enlargement of a section of the red vessel. We have already noticed remarkable alteration of the direction of the blood stream, the heart driving

it back. This is very instructive, because most of the worms (even the Entero-venous) the blood in the dorsal vessel moves from back to front, but in the entomorphs in the opposite direction. As a Ciliolite-worm shuffles suddenly from one direction to the other, it shows us temporarily, in a sense, the phylogenetic transition from the earlier forward direction of the dorsal current (in the worms) to the new backward direction (in the entomorphs).

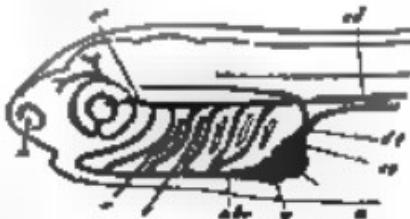


FIG. 245.—Blood-vessels of a Salpophore, with rudimentary vascular system, from the *Vita de Corpus* (section of the anterior and posterior ventral vessel, and anterior ventral branch of the dorsal vessel, and the gill-arches passing between the aorta, pulmonary, and gut. (From Gegenbaer.)

vessels that proceed from either end of the tubular heart acquire dual function.

The foremost section of the ventral vessel henceforth always conveys blood from the heart, and so acts as an artery; the hind section of the same vessel brings the blood from the body to the heart, and so becomes a vein. In view of their relation to the two sections of the gut, we may call the latter the intestinal vein and the former the branchial artery. The blood contained in both vessels, and also in the heart, is venous or carbonated blood—i.e., rich in carbonic acid; on the other hand, the blood entering the gills into the dorsal vessel is provided with fresh oxygen—arterial or oxygenated blood. The finest branches of the arteries

and veins gather in a ventral vessel under the gut (intestinal vein), and pass back to the gills. A number of transverse vascular arches, which effect anastomosis and run in the wall of the branchial gut from belly to back, absorb oxygen & carbonic acid; they communicate with the dorsal vessel. As the dorsal part of the ventral vessel, which also overruns the heart in the Crustaceans, has developed in the Ascidiæ into a simple atrial heart, we may regard the development of this in the Amphioxus as a result of degeneration, a return to this more primitive form of the vascular system.



Fig. 365.—The first arterial arches of the Notochord; the higher parts of the structure disappear, only the shaded parts remain. Letters as in Fig. 366. *a*, aorta; *b*, pulmonary artery; *c*, branches of some of the lower arches; *d*, heart. (From Müller.)

Fig. 366.—The first arterial arches of amphioxus; letters as in Fig. 365. *a*, ventral artery; *b*, dorsal veins passing into each bar to the tissues by means of a net of very fine, ventral, hair-like vessels, or capillaries (Fig. 367).

When we turn from the *T*-cases to the closely-related *Amphioxus* we are astonished at first to find an apparent retrogression in the formation of the vascular system. As we have seen, the *Amphioxus* has no real heart; its colourless blood is driven along in its vascular system by the principal vessel itself, which contracts regularly in its whole length (cf. Fig. 360). A dorsal vessel that lies above the gut (aorta) receives the arterial blood from the gills and drives it into the body. Returning from here,

and it is only in the aorta that the *Ae* really belong to our ancestral *Ae*, not to the regression, but inherited the one-chambered heart of the Prothorontia, and transmitted it directly to the earliest Crustaceans (cf. the ideal Primitive Vertebrates, *Annelida*, Figs. 93-100).

The further phylogenetic evolution of the vascular system is revealed to us by the comparative anatomy of the Crustaceans. At the lowest stage of this group, in the Cyclopoidæ, we find for the first time the differentiation of the vasculature into two sections: a system of blood-vessels proper, which convey the red blood about the body, and a system of lymphatic vessels,

which absorb the colourless lymph from the tissues and convey it to the blood. The lymphatics that absorb from the gut and pour into the blood-stream the milky food-fluid formed by digestion are distinguished by the name of chyle.

While the chyle is a high proportion of fatty particles, the lymph proper is colourless. Both chyle and lymph contain the colourless amoeboid cells (leucocytes, Fig. 32) that we also find distributed in the blood as colourless blood-cells (or "white corpuscles"); but the blood also contains a much larger quantity of red cells, and these give its characteristic colour to the blood of the Craniotes (erythrocytes, Fig. 33). The distinction between lymph, chyle, and blood-stuff which is found in all the Craniotes may be regarded as an

analogous to the venous blood from the body and passes it on to the anterior section, the ventricle. From this it is driven through the trunk of the branchial artery (the foremost section of the ventral vessel

### the Subabill an arterial

developed from the foremost end of the ventricle, as a special division, cut off by valves. It passes into the enlarged head of the trunk of the branchial artery (Fig. 363 abr.). On each side 5-7 arteries proceed from it. These run between the gill-arches, surround the gutlet, and unite above into a common trans-aorta, the continuation of which over the gut corresponds to the dorsal aorta of the worms. As the curved arteries on the gill-arches spread into a network of respiratory capillaries, they



FIG. 363.—Illustrations of the five arterial arches in the embryo of a Vertebrate, shown at different stages. The first arch is the aortic arch, or trunk of artery, of which the first two pairs have disappeared again. To Fig. 363 the common trunk of the first two pairs of arteries is called the aortic arch; + terminal, or ordinary, or ventral or ventral, + posterior.

outcomes of division of labour between various sections of our originally simple vascular system. In the Craniotes—the spleen makes its first appearance, an organ rich in blood, the chief function of which is the extensive formation of new colourless and red cells. It is not found in the Acrania and Cyclostomes, or any of the Invertebrates. It has been transmitted from the earliest fishes to all the Craniotes.

The heart also, the central organ of circulation in all the Craniotes, shows an advance in structure in the Cyclostomes. The simple, spindle-shaped heart-tube, found in the same form in the embryo of all the Craniotes, is divided into two sections or chambers in the Cyclostomes, and these are separated by a pair of valves. The hind section, the ventricle,

conveys venous blood to their lower part (as arteries of the branchial artery) and arterial blood in the upper part (as arteries of the heart). The junctures of the various aortic arches on the right and left are called the roots of the aorta. Of an originally large number of aortic arches there remain at first six, then (owing to degeneration of the fifth arch) only five, pairs; and from these five pairs (Fig. 364) the chief parts of the arterial system develop in all the higher Vertebrates.

The appearance of the lungs and the atmospheric respiration connected therewith, which we first meet in the Diplopoda, is the next important step in vascular evolution. In the Diplopoda the muscle of the heart is divided by an incomplete partition into two halves. Only the right

receives the venous blood from the body. The left side receives the arterial blood from the pulmonary veins. The two auricles have a common opening into the single ventricle,



FIG. 351.



FIG. 352.

(From Ringer.)

FIG. 353.—Heart of the same embryo (Fig. 350) from which the inferior vena cava has been removed. 1, left ventricle; 2, right ventricle; 3, aortal bulb. (From Ringer.)

#### Here the two kinds of blood—

① come or bulk into the arterial arches. From the last arterial arches the pulmonary arteries arise (Fig. 353, 3). These force a part of the mixed blood into the lungs, the other part of it going through the aorta into the body.

From the Diplopoda upwards we notice a progressive development of the tracheal system, which ends finally with the loss of tracheal respiration and a complete separation of the two halves of the circulation. In the Amphibia the partition between the two auricles is complete. In their earlier stages, as tadpoles (Fig. 354), they have still the bronchial respiration and the circulation of the fishes, and their heart contains venous blood alone. Afterwards the lungs and pulmonary vessels are developed, and henceforth the ventricle of the heart contains mixed blood. In the reptiles the ventricle and its arterial cone begin to divide into two halves by a longitudinal partition, and this partition becomes complete in the higher reptiles and birds on the one hand, and the mammals on the other. Henceforth, the right half of the heart contains only venous, and the left half only arterial, blood, as we find in all birds and mammals. The right auricle receives the carbonized or venous blood from the veins of the body, and the right ventricle drives it

through the pulmonary arteries into the lungs. From here the blood returns, as oxygenated or arterial blood, through the pulmonary veins to the left auricle, and is forced by the left ventricle into the arteries of the body. Between the pulmonary arteries and veins is the capillary system of the small or pulmonary circulation. Between the body-arteries and veins is the capillary system of the large or body-circulation. It is only in the two highest classes of Vertebrates—the birds and mammals—that we find a complete division of the circulations. Moreover, this complete separation has been developed quite independently in the two classes, as the abdominal formation of the aortic system of itself. In the birds the right half of the fourth arterial arch has become the pulmonary arch (Fig. 355). In the mammals this has been developed from the left half of the same fourth arch (Fig. 356).

If we compare the fully-developed arterial systems of the various classes of vertebrates, we see a good deal of variety, yet it always proceeds from the fundamental type. Its development



FIG. 354.



FIG. 355.

FIG. 356.—Heart and head of a frog (Rana temporaria) at a later stage. (After Ringer.)

FIG. 357.—Heart of the same embryo, from which a portion of the venae cavae has been removed. (From Ringer.)

just the same in man as in the other mammals; in particular, the modification of the six pairs of arterial arches is the same in both (Figs. 357-370). At first there is only a single pair of arches, which

## EVOLUTION OF THE CARDIAC SYSTEM

lie on the inner surface of the first pair of gill-arches. Behind this there then develop a second and third pair of arches (lying on the inner side of the second and third gill-arches, Fig. 367). Finally, we



Fig. 367.



Fig. 368.

Fig. 368—Heart of a human embryo, four weeks old. Shows 3 pairs of arches, a ventral, and right half of the dorsal, connected by a dorsal aorta, a left ventricle, a right atrium, an arterial bulb, superior vena cava, and right and left aortic arches of the intercardiac vein. (From Kühn.)

Fig. 369—Heart of a human embryo, eight weeks old. Shows 3 pairs of arches, a right atrium, a left atrium, a dorsal aorta, a right and left aortic arches, and the two brachiocephalic veins. (From Kühn.)

The heart of a human embryo, eight weeks old, shows 3 pairs of arches, a right atrium, a left atrium, a dorsal aorta, a right and left aortic arches, and the two brachiocephalic veins. (From Kühn.)

get a fourth, fifth, and sixth pair. Of the six primitive arterial arches of the Amniotes three soon pass away (the first, second, and fifth), of the remaining three, the third gives the carotid, the fourth the aorta, and the sixth (number 5 in Figs. 364 and 368) the pulmonary arteries.

The human heart also develops in just the same way as that of the other mammals (Fig. 370). We have already seen the first rudiments of its embryology, which in the main corresponds to amphibia (Figs. 369, 370). We saw that the palingenetic form of the heart is a spindle-shaped thickening of the gut-layer in the ventral wall of the head-gut. The structure is then hollowed out, forms a simple tube, detaches from its place of origin, and henceforth lies freely in the cardiac cavity. Presently the tube bends into the shape of an S, and turns spirally on an imaginary axis in such a way that

the blind part comes to lie on the dorsal surface of the free part. The united ventricle opens into the posterior end. From the anterior end spring the aortic arches.

The first structure of the human heart, showing a very simple early, corresponds to the tunicae-heart, and is a reproduction of that of the Prechordians, but it now divides into two, and subsequently into three, compartments; this reminds us for a time of the heart of the Cetaceans and fishes. The spiral twisting and bending of the heart increases, and at the same time two transverse constrictions appear, dividing it externally into three sections (Figs. 371, 372). The foremost section, which is turned towards the ventral side, and from which the aortic arches rise, reproduces the arterial bulb of the Selachii. The middle section is a simple ventricle, and the hindmost, the earliest formed (so far the dorsal side, upon which the trachea, lungs, oesophagus, &c., are placed) is a simple atrium (or atrium). The latter forms, like the simple atrium of the fish-heart, a pair of lateral dilatations, the

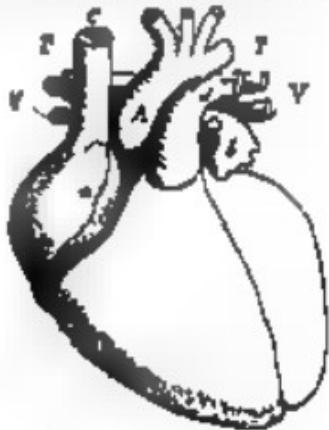


Fig. 370—Heart of the adult man, fully developed. Shows liver, ventral aorta, a right auricle (dorsal half of the right ventricle), a left auricle (ventral half of the left ventricle), a superior vena cava, V. pulmonaria, V. hemiazygos, A. pulm. dext., A. aorta. (From Müller.)

auricles (Fig. 371 & 372); and the constriction between the atrium and ventricle is called the atrioventricular canal (Fig. 372 a). The heart of the human embryo is now a complete fish-heart.

In perfect harmony with its phylogeny, the embryonic development of the human heart shows a gradual transition from the fish-heart, through the amphibia and reptile, to the mammal form. The most important point in the transition is the formation of a longitudinal furrow in the

of the heart into right (ventral) and left (arterial) halves (cf. Figs. 373-374). The "separates" the right and left half, each of which absorbs a preceding auricle, into the right auricle open the body-veins (upper and lower vena cava, Figs. 375 & 327 a); the left auricle receives the pulmonary veins. In "injurious" entomologist

The heart of all the Vertebrates belongs originally to the hyposoma of the head, and we accordingly find it in the embryo of man and all the other Amniotes right in front on the under-side of the head; just as in the fishes it remains permanently in front of the gut-tube. It afterwards

turns round, with the aorta

segment of the heart, and at last reaches the breast, between the two lungs. At first it symmetrically in the middle of the body, so that its long axis corresponds

tion. But in the apes the axis begins to be oblique, and the apex of the heart to move towards the left side. The dis-



FIG. 375.—Transverse section of the heart of a chick embryo, four hours old. (From Müller's *Entwickelung des menschlichen Herzens*, 2<sup>nd</sup> edn., p. 11.) The atrium (at) receives the superior and inferior venae cavae (v.c.). The aorta (a.) arises in the atrium (at) and passes through the ventricle (vtr) to the bulbus arteriosus (ba.). The epicardial layer of the ventricle (epicardial layer) is the outer (endocardial?) wall of the heart, the two unlabelled ventricles being also separated by the endocardial capsule (c.) of the atrium, or auricle.

surface is soon seen in the ventricle (Fig. 326 a). This is the external sign of the internal partition by which the ventricle is divided into two—a right venous and left arterial ventricle. Simultaneously a longitudinal partition is formed in the dorsal section of the primitive fish-like heart, the arterial bulb, externally indicated by a longitudinal furrow (Fig. 326 a'). The cavity of the bulb is divided into two internal halves, the pulmonary-artery bulb, that opens into the right ventricle, and the aorta-bulb, that opens into the left ventricle. When all the partitions are complete, the small (pulmonary) circulation is distinguished from the large (body) circulation; the motive centre of the former is the right half, and that of the latter the left half, of the heart.

placement is greatest in the anthropoid apes—chimpanzee, gorilla, and orang—which resemble man in this.

As the heart of all Vertebrates is originally, in the light of phylogeny, only a local enlargement of the middle principal vein, it is in perfect accord with the biogeographic law that its first structure in the embryo is a simple spindle-shaped tube in the ventral wall of the head-gut. A thin membrane, standing vertically in the middle place,

II of the head-gut with the lower broad-wall. As the tube extends and detaches from the gut-wall, it divides the mesocardium into an upper (dorsal) and lower (ventral) plate (usually called the *mesocardium dorsale* and *mesocardium ventrale* in man, Fig. 379 a,b).

## EVOLUTION OF THE VASCULAR SYSTEM

pericardium off his two lateral cavities, Rammik's "neck-cavities" (Fig. 329 A). These cavities afterwards join and form the simple pericardial cavity, and are therefore called by Knöller the "primitive pericardial cavity."

The double cervical cavity of the Amniotes is very interesting, both from the anatomical and the evolutionary point of view; it corresponds to a part of the hypobranchials of the head of the lower Vertebrates—that part of the ventral mesopouch.

With the "visceral cavities" below. Each of the cavities still communicates freely behind with the two oesophago-pertitoneal

to be pushed outwards as in rupture (cf. Fig. 329 A). A transverse fold of the ventral wall, which receives all the veins that open into the heart, grows up from below between the pericardium and the stomach, and forms a transverse partition, which is the first structure of the primary diaphragm (Fig. 329 A). This important muscular partition, which completely separates the thoracic and abdominal cavities in the mammals alone, is still very imperfect here; the two cavities still

join. These canals, which belong to dorsal part of the head-column, and

which we may call briefly *visceral ducts*,—the two pulmonary ducts, which develop from the fund end of the ventral a.s. of the head-gut; they thus become the two pleural cavities.

The diaphragm makes its first appearance in the class of the Amphibia (in the Anabatrachians) as an insignificant muscular transverse fold of the ventral wall, which

... lies from the fore end of the transverse abdominal muscle, and grows between the pericardium and the liver. In the reptiles (lizards and crocodiles) a later dorsal part is joined to this earlier ventral part of the rudimentary diaphragm, a pair of subvertebral muscles rising from the vertebral column and being added as "extensors" to the transverse partition. But it was probably in the Permian mammals that the two originally separate parts were united, and the diaphragm became a complete partition between the thoracic and abdominal cavities in the mammals; as it considerably enlarges the chest-cavity when it contracts, it becomes an important respiratory muscle.

The ontogeny of the diaphragm in man and the other mammals reproduces this phylogenetic process to-day, in accordance with the biogenetic law, in all the mammals the diaphragm is formed by the secondary conjoining of the two originally separate structures, the anterior ventral part and the later dorsal part.

Sometimes the blending of the two diaphragmatic structures, and consequently the separation of the one pleural duct from the abdominal cavity, is not completed in man. This leads to a diaphragmatic rupture (*tertius diaphragma*). The two cavities then remain in communication by an open pleural duct, and loops of the intestine may penetrate by this "rupture opening" into the chest-cavity. This is one of those



FIG. 329.—Primit. ventral of a human embryo, approximately at mid-stage of the third month. (After Knöller, "Kunst der Amnionbildung," and modified by Knöller.) The diagram shows the early development of the diaphragm, a transverse fold of the ventral wall, separating the thoracic cavity above from the abdominal cavity below. The diagram also shows the amniotic cavity (Am), rectal tube (re), allantois (ar), and urinary bladder (ur).

the trunk; and, just as above afterwards coalesce into a simple body-cavity (the ventral mesentery disappearing), we had the same thing happening in the head. This simple primary pericardial cavity has been well called by Gegenbaur the "head-cavities," and by Knöller the "pericardial breast-cavity." As it now encloses the heart, it may also be called *cardiac*.

The cardiac, or head-cavities, is often disproportionately large in the Amniote, the simple cardiac tube growing considerably and lying in several folds. This causes the ventral wall of the amniote ventricle between the head and the ventral

fatal mis-growth that shows the great part that blind chance has in organic development.

Thus the thoracic cavity of the mammal, with its important contents, the heart and

lungs, belongs originally to the head, which is double, as is

shown, in all the Amniotes, and the simple apertio-shaped cardiac tube, which

— looks like a —

point, is only formed at a later stage, when the two lateral tubes move backwards, touch each other, and effect continuity in the middle line. In man, as in the rabbit, the two embryonic hearts are still far apart at the stage when there are already eight primitive segments (Fig. 374 A). So also the two *coelom-pouches* of the head in which lie

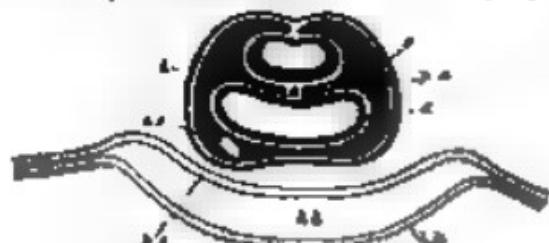


FIG. 374.—Transverse section of the head of a quaternary (quadruped) larva at the stage when the heart and lungs have entered the body-cavity.

lungs belongs originally to the head of the vertebrate body, and its enclosure in the trunk is secondary. This instructive and very interesting fact is entirely proved by the concordant evidence of comparative anatomy and ontogeny. The lungs are outgrowths of the head-gut; the heart develops from its inner wall. The glottal sacs that enclose the lungs are dorsal parts of the head-coelom, originating from the pharyngeal wall in the shape of a small patch-like outgrowth, but soon grows so large that, in order to find room, it has to pass far behind into the trunk-cavity. To put it more precisely, the lung of the quadrupeds retains this hereditary growth-process of the fishes; for the hydrostatic floating bladder of the latter is the air-filled organ from which the air-breathing organs of the latter have been evolved.

There is an interesting comparative phenomenon in the formation of the heart

from the embryonic vesicle that the separate lateral structures join together, and finally combine in the middle line. As the median partition between the right and left cardiotic ducts disappears, the two cervical cavities freely communicate (Fig. 375), and from, on the ventral side of the amniote head, a horse-shoe-shaped arch, the points of which advance backwards like the pterygoids or pteryloid canals, and from there into the two peritoneal sacs of the trunk. But even after the combination of the cervical cavities (Fig. 376) the two cardiac tubes remain separate

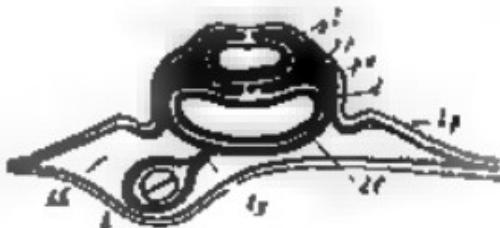


FIG. 375.—Transverse section of the median region of the head of a quaternary (quadruped) larva. In the cervical cavity (1) the heart (2) is well covered by a mesentery (4a) with the peritoneal layer (4b), a peritoneal layer, of peritoneal plane, a membrane which is homologous to the serous plane, Ap. first rise of the pterygoid arch (3).

at first; and even after they have united a delicate partition in the middle of the simple endothelial tube (Figs. 379 A, Fig. B) indicates the original separation. This comparative "primary cardiac sep-

tum" presently disappears, and has no relation to the subsequent permanent partition between the halves of the heart, which, as a heritage from the embryo, has a great phylogenetic importance.

Thorough opponents of the biogenetic law have laid great stress on these and similar congeneric phenomena, and endeavoured to urge them as striking disproofs of the law. As in every other instance, careful, discriminating, comparative-morphological examination converts these supposed disproofs of evolution into strong arguments in its favour. In his excellent work, *On the Structure of the Heart in the Amphibia* (1884), Carl Rabl has shown how easily these certain congeneric facts can be explained by the secondary adaptation of the embryonic

structure to the great extension of the fluid-gels.

The embryology of all the other parts of the vascular system also gives us abundant and valuable data for the purpose of phylogeny. But as one needs a thorough knowledge of the intricate structure of the whole vascular system in man and the other Vertebrates in order to follow this with profit, we cannot go into it further here. Moreover, many important features in the ontogeny of the vascular system are still very obscure and controversial. The characters of the embryonic circulation of the Amniotes, which are here previously mentioned (Chapter XV.), are late acquisitions and entirely eompsic. (CC pp. 170-171; Figs. 321-322.)

## CHAPTER XXIX. EVOLUTION OF THE SEXUAL ORGANS

If we measure the importance of the systems of organs in the animal frame according to the richness and variety of their functions and the physiological interest that this implies, we must regard as one of the principal and most interesting systems that one which we are now going to examine—the systems of the reproductive organs. Just as nutrition is the first and most urgent condition for the self-maintenance of the individual organism, so reproduction alone secures the maintenance of humanity—or, rather, the maintenance of the long series of generations which the totality of the organic stem represents in their genealogical connection. No individual organism has the prerogative of immortality. To each is allotted only a brief span of

million-year course of the  
of life.

Hence, reproduction and the correlated phenomenon, heredity, have long been regarded, together with nutrition, as the most important and fundamental functions of living things, and it has been attempted to distinguish them from "lifeless bodies" on this very score. As a

matter of fact, this division is not so profound and thorough as it seems to be, and is generally supposed to be. If we examine carefully the nature of the reproductive process, we soon see that it can be reduced to a general property that is found in inorganic as well as organic bodies—growth. Reproduction is a regeneration and growth of the organism beyond the individual limit, which raises a part of it into the whole. This is most clearly seen when we study it in the simplest and lowest organisms, especially the Monera (Figs. 246-247) and the unicellular Amnebec (Fig. 27). There the single individual is a single plastid. As soon as it has reached a certain limit of size by continuous feeding and normal growth, it cannot pass it, but divides, by binary fission, into two equal halves. Each of these half-independent life, and so

each reaches the limit of growth, and divides. In each of these acts of self-cloning two new centres of attraction are formed for the particles of bodies, the founders of the two new-formed individuals. There is no such thing as immortality even in these unicellular

The last point we speak is connected to the art of claspers (cf. p. 44).

In many other Protozoan reproduction takes place not by division, but by budding (fission). In this case the growth that determines reproduction is not total (as in regeneration), but partial. Modern reproduction, also we may suppose the legal group-product, that happens in a new individual in the bud, as a child-organism is the parent-organism from which it is derived. The latter is older and larger than the former. Inasmuch the two subjects are equal in age and morphological value. Next to generation are here, as other forms of sexual reproduction, the forming of male and female and the breeding of embryonic cells. But the latter leads us at once to sexual development, the characteristic feature of which is the importance of the sexes. I have already talk those various types of reproduction in my *History of Evolution* (chap. viii.) and my *Evolution of Life* (chap. vi.).

The earliest ancestors of man and the higher animals had no faculty of sexual reproduction, but multiplied solely by fission—either asexual generation, or the formation of eutyrocytic buds or cells, as among Protozoa and so on. The differentiation of the sexes came at a later stage. We see this most plainly in the Protozoa in which the cells of one individual produce the continuous change of the hereditary organism (aberrant regeneration and permanent separation of the hereditary). We may say that in this case the germ is (the condition of regeneration) is retained in the calyxes of the two daughter cells with a single, abnormally large bud-bladd. At the same time the portions of the two germs show a separation of the plan. As for the daughter cells are quite homogeneous, but different selection — brings about a marked contrast between them — larger female cells (merosomes) and smaller male cells (microsomes). It used to be a great advantage in the struggle for life for the new individual to have inherited different qualities from the two older parents. The further history of the contrast between the daughter cells led to sexual differentiation. One cell becomes the female organ (merosome), and the other the male organ (microsomes).

The simplest form of sexual reproduction among the living beings we find in the *Ciliates* (p. 252). The lower

group, the *Amoebidae*, *Paramecium*, *Hydro*, and other Ciliates of the lowest rank Protoplasts (Fig. 252). Oxytrichids (Fig. 253), Hydro, etc., are very simple heterotrichous, the thin wall of which consists (as in the ciliates generally) only of the two primary germinal layers. As soon as the body reaches sexual maturity, a number of the cells by its will become female sex, and others male spermatocysts; the former having very large, as they possess a considerable quantity of yolk-principle in their protoplasm (Fig. 254); the latter are very small in amount of their required chlorine, and change and divide continually (spermatogenesis). On such basis of cells derived from this stage of origin, the primary germinal layers, full either sex, the protostomia move on into the cavity of the gut and unite there by living together. This is the monogamous process of formation, which we have discussed in the ninth Chapter (cf. Fig. 255).

From these simplest forms of sexual propagation, as we see above that today in the living *Zoothetes*, the *Gymnophora*, *Spongidae*, and *Tulipae*, we gather some important data. In the first place, we learn that primary division, without a nucleus for sexual reproduction except the fusion of recipient of one different cells — a female ovum and male sperm-cell. All other Sponges, and all the very complex phenomena that accompany the sexual act in the higher animals, are of a secondary and secondary character and are later additions to this simple, primary process of copulation and fecundation. But if we look no more here relatively important part the evolution of the two main lines of the whole of organic nature, or the life of plants, of animals, and of men, how the mutual interaction of the sexes, here, is the distinguishing of the most remarkable process. In fact, one of the chief material means of the highest development of life—we cannot too greatly emphasize that tracing of love to its source, the ultimate form of two cells.

Throughout the whole of living nature the greatest effects produced from this very small —. Consider the fact that the flower, the sexual organ of the flowering plants, play is nature, or the existence of wonderful phenomena that exceed anything that occurs in animal life; or the

however . . . influence of love in the life of man. In every case the fusion of two cells is the sole original creative power; in every case this invisible process profoundly affects the development of the most varied structures. We may say, indeed, that no other organic process can compare to it for its wide

profoundness and intensity of . . .

. . . is not the Socratic myth of Julian and Cleo, the old Greek legend of Paris and Helen, and so many other famous traditions, only the poetic expression of the vast influences that love selection have exercised over

of history, over even the other past

agitate the heart

tripped in their joint influence by the sense-inflaming and mind-exalting drugs. On the one hand, we look to love with gratitude as the source of the greatest artistic achievements—the noblest creations of poetry, plastic art, and music; we see it as the chief factor in the moral advances of humanity, the foundation of family life, and therefore of social advance. On the other hand, we dread that the devouring flame that brings destruction to so many, and has caused more misery, vice, and crime than all the other evils of human life put together. The wonderful is love and its enormous influence on the life of the soul, or on the different functions of the cerebriform type, that have more than anywhere else the "supernatural" result, seems to make any attempt at natural explanation. Yet comparative evolution leads us closely and indubitably to the first source of love—affinity of two different erotic cells, the sperm-cell and ovum."

The lowest Metazoa throw light on this very simple origin of the otherwise phantasmal reproduction, and they also teach us that the earliest sexual form was hermaphroditism, and that the separation of the sexes (by division of labor) is a secondary and later phenomenon.

"Hermaphroditism predomini-

nates among groups of the low

most sexually-matured individuals, such persons, containing female and male sexual cells, and is therefore able to fertilize itself and reproduce. Thus we find our

and spores-cells in the same individual, not only in the lowest Zoophytes (Gastropods, Sponges, and many Polyps), but also in many worms (leeches and earthworms), many of the molluscs and cephalopods, brachiopods, and corals. All of

the Gastrulae up to the Proterostomes were hermaphrodites, possibly even the earliest Acrania.

Let me give an instructive proof of this remarkable . . .

genera of fishes are still hermaphrodites, and that it is occasionally found in the higher Vertebrates of all classes (as turtles). We may conclude from this that gonochorism (separation of the sexes) was a later stage in our development. At first, male and female individuals differ only in the presence of one or other kind of glands; in other respects they were identical, as we still find in the Amphioxus and the Cyclostomes. Afterwards, accessory organs (ovaria, etc.) are associated with the primary sexual glands; and much later again sexual selection has given rise to the secondary sexual characters—those differences between the sexes which do not affect the sexual organs themselves, but other parts of the body (such as the man's beard or the woman's breast).

The third important fact that we learn from the lower Zoophytes relates to the earliest origin of the two kinds of sexual cells. As in the Gastrulae (the lowest sponges and Hydrozoa), in which we find the first indications of sexual differentiation, the whole body consists merely of

casted from the cells of these primary layers, either the inner or outer, or from both. This simple fact is extremely important, because the first trace of the ovum, as well as the spermatogenesis, is found in the middle germinal layer or mesoderm in the higher animals, especially the Vertebrates.

development from . . .

coincides with the secondary formation of the mesoderm.

If we trace the phylogeny of the sexual organs in our earliest Vertebrates, we see,

that the lowest Craniotaria (*Cephaloscyllium, Platycephalus*) exhibit it to us, we find that the first step in advance is the localization or organization of the two kinds of sexual

altered in the epithelio-mesodermic layer, the Spermatogonia and the detached testicular germinal layers, and become functionally differentiated.

In the Crinoids and Platyodes we find these associated in groups which we call sexual glands (*glands*). We can now for the first time speak of sexual organs in the morphological sense. The female germinative glands, which in this stage form merely groups of homogeneous cells, in the ovaries (Fig. 241 A). The male germinative glands, which also in their first form consist of a cluster of spermatocytes, are the testicles (Fig. 242 A). In the medusae, which descended both ontogenetically and phylogenetically from the more simply organized Polype, we find these simple sexual glands somewhat as

that appear at the edge of the primitive mouth (right and left), as a rule during gastrulation or immediately afterwards—the important promesoblasts, or “polar cells of the mesoderm,” or “primitive cells of the middle germinal layer” (p. 242). In the vital Enterocoela, in which the mesoderm appears from the first in the shape of a couple of coelom-pouches, there are very probably the original gonads (p. 244). This is seen very clearly in the arrow-worm (*Sagitta*). In the spiculae of *Sagitta* (Fig. 383, A) we find at an early stage a couple of entodermic cells of an unusual size (Fig.) at the base of the primitive gut (Fig.). These primitive sexual cells (*Argonadites*) are symmetrically placed to the right and left of the midline plane, like the two promesoblasts of the bilateral gastrula of the Amphioxus (Fig. 36 A, p. 86). A little



Fig.—Stages of *Sagitta*. *A*, early stage of development. (*From Nittony*) *B*, open primary mouth. *C*, the two oral primordia meet above, so forming gut & primary mouth. (*After Nittony*) *a*, anterior; *b*, dorsal; *c*, ventral; *d*, postero-dorsal; *e*, postero-ventral; *f*, posterior layer; *g*, ventral layer of brain; *h*, peritoneal gut (mesenteron); *i*, mesoderm (mesenteron).

gastric pouches, sometimes as evaginations of the mid-digestive canal that proceed from the stomach. Particularly interesting in connection with the question of the first origin of the gonads are the lowest forms of the Platyodes, the Crayfishes that have of late been separated as a special class (*Platyodes*) from the Trilobites proper (Fig. 239). In these very primitive Platyodes the two pairs of sexual glands are merely two pairs of rows of differentiated cells in the entodermic wall of the primitive gut—two median ovaries (*o*) within, and two testical spermataries (*t*) without. The mature sexual cells are selected by the posterior testicles; the female (*f*) lies in front of the male (*m*).

In the great majority of the Bilateria, or Coelomaria it is the mesoderm from which the gonads develop. Finally the first traces of them are the two large cells

outwards from, then the two coelom-pouches (*B*, *or*) are developed out of the primitive gut, and each propagates divides into a male and a female sexual cell (*B*, *g*). The two male cells (at first rather the finger) lie close together within, and are the parent-cells of the testicles (*prostergonites*). The two female cells lie outwards from these, and are the parent-cells of the ovary (*protoovaria*). Afterwards, when the coelom-pouches have detached from the permanent gut (*C*, *d*) and the primitive mouth (*A*, *M*) is closed, the female cells advance towards the mouth (*C*, *st*), and the male towards the rectum. The foremost pair of ovaries are then separated by a transverse partition from the hind pair. Thus the first structures of the sexual glands of the Sagittæ are a couple of hermaphroditic anamniotic cells; each of these divides

## EVOLUTION OF THE SEXUAL ORGANS

into a male and a female cell; and these four cells are the parent-cells of the four sexual glands. Probably the two primordial blastulae of the Amphioxus-gastrula (Fig. 35) are also hermaphroditic primitive sexual cells in the same sense, inherited by this earliest vertebrate from its ancient bilateral gasterostome ancestors.



FIG. 36.—A Part of the Blasozoa of Amphioxus. A, a longitudinal section of the body showing the gonad (stippled), the digestive tract, &c., & the nervous system. B, a transverse section of the body, showing the gonad (stippled), the nervous system, & the digestive tract. From J. H. Parker (Myogenesis).

The sexually-mature Amphioxus is not hermaphroditic, as its nearest invertebrate relatives, the Tunicates, are, and as the long-extinct pre-Silurian Primitive Vertebrates (*Proscopodylus*, Figs. 98-102) probably was. The actual larva has gonochoristic structures of a very interesting kind. As we saw in the anatomy of the Amphioxus, we find the ovaries of the female and the spermataries of the males in the shape of twenty to thirty pairs of elliptical or rounded four-cornered nests,

which lie on either side of the gut on the ventral surface of the respiratory pore (Fig. 109 g'). According to the important discovery of Ruckert (1888), the sexual glands of the parent fishes, the Selachii, are similarly arranged. They only unite afterwards to form a pair of simple gonads. These have been transmitted by heredity to all the rest of the Craniotes. In every case they lie originally on each side of the mesentery, underneath the chorda, at the bottom of the body-cavity. The first traces of them are found in the coelocoelomites, at the spot where the skin-flap layer and gut-flap layer meet in the middle of the mesenteric plate (Fig. 93 a'). At this point we observe at an early stage in all craniote embryos a small string-like cluster of cells, which we may call, with Waldeyer, the "germ epithelium," or (in harmony with the other plate-shaped rudimentary organs) the *sexual plate* (Fig. 173 a). This germinal or sexual plate is found in the fifth week in the human embryo, in the shape of a couple of long whitish streaks, on the inner side of the primitive kidneys (Figs. 183 a). The cells of this sexual plate are distinguished by their cylindrical form and chemical composition from the rest of the coelom-cells; they have a different purpose from the flat cells which line the rest of the body-cavity. As the germ epithelium of the sexual plate becomes thicker, and supporting tissue grows into it from the mesoderm, it becomes a rudimentary testis-gland. This sexual gland then develops into the ovary in the female Craniotes, and the testes in the male.

In the formation of the gonidia or erotic sexual cells and their conjunction at fecundation we have the sole essential features of sexual reproduction; but in the great majority of animals we find other organs taking part in it. The chief of these secondary sexual organs are the gonoducts, which serve to convey the matured sexual cells out of the body, and the copulative organs, which bring the fecundating male sperm into touch with the ovum-bearing female. The latter organs are, as a rule, only found in the higher animals, and are much less widely distributed than the gonoducts. But those who are secondary formations, and are wanting in many animals of the lower groups.

In the lower animals the mature sexual cells are generally ejected directly from

the body. Sometimes they pass out immediately through the skin (Hydra and many hydrozoans); sometimes they fall into the gastric cavity, and are evacuated by the mouth (gastropods, sponge, many medusae, and corals); sometimes they enter the body-cavity, and are ejected by a special pore (*porus genitulus*) in the ventral wall. The latter procedure is found in many of the worms, and also in the lowest Vertebrates. Amphioxus has the peculiar feature that the mature sexual products fall first into the mantle-cavity; from there they are either evacuated by the respiratory pore, or else they pass through the gill-slits into the branchial gut, and so out by the mouth (p. 182). In the Cyclostomes they fall into the body-cavity, and are ejected by a genital pore in its wall; so also in some of the fishes. From these we gather the fact

to convey the sexual products, and this had originally a totally different function —namely, the system of urinary organs. These organs have primarily the sole duty of removing unusable matter from the body in a fluid form. Their liquid excretory product, the urine, is excreted directly through the skin or through the last section of the gut. It is only at a later stage that the tubular urinary passages also convey the sexual products from the body. In this way they become "seed ducts." This remarkable secondary coöperation of the urinary and sexual organs into a common urogenital system is very characteristic of the *Comptitans*, the six higher classes. It is wanting in the lower classes. In order to appreciate it fully, we must give a comparative glance at the structure of the u.



<sup>2</sup> The following section of the argumentation shows a similar, but more logical and, I think, more plausible case, of course. I have done this, partly, to emphasize the importance of the argument, but also, to demonstrate the general character of the book.

tions of our earlier ancestors in this respect. On the other hand, in all the higher and most of the lower Vertebrates (and most of the higher Invertebrates) we find in both sexes special tubular processes of the sexual gland, which are called "genoducta." In the female they conduct the ova from the ovaries, and are called "oviducts," or "Fallopian tubes." In the male they convey the spermatozoa from the testicles, and are called "seminal ducts," or "vasa deferentia."

The original and genetic relation of these two kinds of ducts is just the same in space as in the rest of the higher Vertebrates, and quite different from what we find in most of the Invertebrates. In the latter, as a rule, the gonoducts develop directly from the embryonic glands or from the outer skin; but in the Vertebrates an independent organic system is employed

The renal or urinary system is one of the oldest and most important systems of organs in the differentiated animal body, as it has pointed out on several previous occasions (cf. Chapter XVII). We find it not only in the higher Metazoa, but also very generally distributed in the earliest group of the Vermiformia. Here we meet it at the lowest worms, the Rotatoria (Gastropoda, Fig. 84), and in the instructive stems of the Platodes. It consists of a pair of simple or branching canals, which are lined with one layer of cells, absorb soluble juices from the tissue, and eject them by an outlet in the outer skin (Fig. 820). Not only the free-living Turbellaria, but also the parasitic Suctoria, and even the still more degenerate tapeworms, which have lost their alimentary canal as consequence of their parasitic life, are equipped with these renal canals.

or nephridia. In the first embryonic structure they are merely a pair of simple cutaneous glands, or depressions in the ectoderm. They are generally described as excretory organs in the worms, but



Fig. 55.—Diel's urinary protoblasts (hydros) of a Planaria larva. The head end of the larval body is seen from the ventral side and covered with the ciliated layer of the epidermis which is here worn off and drawn out to show the apposition with the primitive urinary vesicle (o.) of a planarian larva.

formerly often as "water vessels." They may be conceived as largely-developed tubular cutaneous glands, formed by invagination of the cutaneous layer. According to another view, they

nephridium has no lower opening (with cilia) into the body-cavity and not more one on the epidermis.

In these lower, unsegmented worms, and in the unsegmented Mollusca, there is only one pair of renal ducts. They are more numerous in the higher Articulates. In the Annelids, the body of which is composed of a large number of joints, there is a pair of these pronephridia in each segment (hence they are called segmental canals or organs). Even here they are still simple tubes; on account of their coiled or looped form, they are often called

"looped canals." In most of the Annelids, and many of the Vermiforms, we can distinguish three sections in the nephridium—an outer muscular duct, a glandular middle part, and an inner part that opens by a ciliated funnel into the body-cavity. This opening is furnished with whirling cilia, and can, therefore, take up the poisons to be excreted directly from the body-cavity and convey them from the body. But in these worms the sexual cells, which develop in very primitive form on the inner surface of the body-cavity, also fall into it when mature, and are sucked up by the funnel-shaped inner ciliated openings of the renal canals, and excreted—*thus*. Thus the urin-

arily different from these segmental canals of the Annelids. The peculiar development of it and its relations to the sexual organs are among the most difficult problems in the morphology of our class. If we examine briefly the vertebrate renal system from the phylogenetic point of view, it is confirmed by our

present knowledge in three

ways: (1)

types of pro-

totrophic kidney-

vesicles.

(2) Types of

kidneys.

These

of kidneys

are not

homologous and

completely distinct, as earlier students (such as Temm) strongly supposed; they represent three different generations of one and the same excretory apparatus; they correspond to three phylogenetic stages,

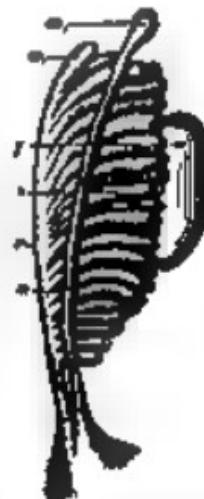


Fig. 56.—Primitive kidney of a Planaria larva. A, the urinary vesicle of the primitive kidney; B, Wallian duct of segmental end of the kidney; C, Wallian duct of segmental end of the kidney; D, renal canal (or nephridium); E, renal gland (or glomerulus).

and succeed each other in the stem-history of the Vertebrates in such wise that the older and more advanced generation develops further behind in the body, and replaces the older and less

the history of our stem, and, consequently, in the natural classification of the Vertebrates.

As in the morphology of any other system of organs, so in the case of the urinary and sexual organs the Amphioxus is the real typical primitive Vertebrate; it affords the key to the mysteries of the structure of man and the higher Vertebrates. The kidneys of the Amphioxus—first discovered by Bovier in 1860—are typical “fæna kidnays,” composed of a double row of short segmental canals (Fig. 573). The inner aperture of these



FIG. 573.—Amphioxus. Cross-section of an 18-hr. old frog embryo, 10 mm. long, the ventral side (anterior) to the right. 1, dorsal aorta; 2, neural tube; 3, dorsal afferent renal tubule; 4, dorsal vena cava; 5, dorsal afferent glomerular artery; 6, dorsal afferent glomerular vein; 7, dorsal afferent tubule; 8, dorsal afferent glomerulus; 9, dorsal afferent glomerular artery; 10, dorsal afferent glomerular vein.

advanced generations that precede it in time and space. The *five kidneys*, first accurately described by Wilibaldo Müller in 1853 in the Cyclostomes and Teleostyes, form the anti-excretory organ of the *Agnatha* (*Agnathous*); they continue in the Cyclostomes and some of the fishes, but are found only in slight traces and for a time in the embryos of the six other classes of Vertebrates. The *posterior kidneys* are first found in the Cyclostomes, behind the *fore kidneys*; they have been transmitted from the *Selachii* to all the Gnathostomes. In the *Agnathous* they act permanently as urinary glands; in the *Agnathous* their anterior part (“*garnetid kidneys*”) changes into organs of the sexual apparatus, while the third generation develops from the end of their posterior part (“*urid kidneys*”)—the characteristic after or permanent kidneys of the three higher classes of Vertebrates. The order in which the three renal systems succeed each other in the embryo of man and the higher Vertebrates corresponds to their phylogenetic



FIG. 574.—Domestic embryo of the 5th week, posterior half of the body. Longitudinal section, seen from the ventral side (the anterior ventral wall, A, is removed; the body cavity, C, opened). 1, gut (rectum); 2, dorsal afferent renal tubule; 3, middle brain; 4, optic nerve; 5, optic chiasm; 6, optic ganglion; 7, pulmonary sac; 8, proventriculus; 9, ventral afferent glomerular artery; 10, glomerulus. (From Allman.)

mesonephros opens into the mesodermic body-cavity (the middle part of the coelom, B); the ventral aperture into the ectodermic mesentery or peribranchial cavity (C). Their position, their

structure, and their relation to the branchial vessels makes it clear that these segmental pronephridia correspond to the rudimentary fore kidneys of the Crustacea. The mouth-cavity into which

drain it opens from the set (*c*). The primitive renal capillae (*mesonephridia*) are distinguished by this out-formation from their predecessors.

In the Nematoda also we find a longitudinal row of segmental canals on each side, which open outwards into the primitive renal ducts (see Abbott, p. 149). The segmental canals (a pair in each segment of the middle part of the body) open indirectly by a ciliated funnel into the body-cavity. From the posterior



FIG. 384.

Fig. 384 of 3 segmental canals, a primitive renal duct, and a ciliated funnel opening into the body-cavity for a pair of renal ducts in the Nematoda (see Abbott, p. 149). The renal ducts are the primitive kidneys, which are the excretory organs of the present kidneys. (From Cope.)

they open seems to correspond to the primitive duct of the latter.

The next higher Vertebrates, the Cyclostomes, yield some very interesting data. Both orders of this class, the lampreys and hagfishes, have lost the fore kidneys inherited from the Annelids—the former permanently, the latter in their earlier stages. Behind them the primitive kidneys soon develop, and in a very characteristic form. The remarkable structures of the mesonephros of the Cyclostomes, discovered by Jules Muller, explain the intricate formation of the kidneys in the higher Vertebrates. We find in the hag-fishes (*Selachiorhina*) a long tube, the proventral duct (*mesonephrostome*, Fig. 384 *a*) This opens with its anterior end into the ectoderm by a ciliated aperture, and externally with its posterior end by an outlet in the skin. Inside it open a large number of small transverse canals ("segmental or primitive urinary canals," *b*). Each of these terminates blindly in a vesicular capsule (*c*), and this encloses a coil of blood-vessel (*glomerulus*), an arterial network, Fig. 384 *B*, *c*. Afferent branches of arteries conduct arterial blood into the coiled branches of the glomerulus (*d*), and efferent arterial branches con-

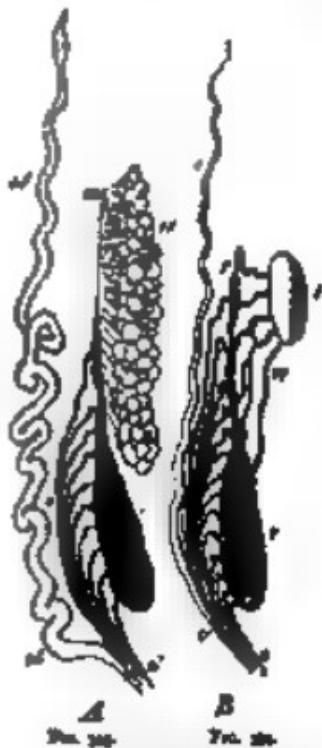


FIG. 385. *A*—Urinary and sexual organs of *Selachiorhina* (Cyclostome or Vertebrate). *B*—Diagram of a single pair of a cyclostome primitive kidney, or kidney of a lamprey and a hag-fish, both showing the nature of a "lumen tubularis" (a lumen tubularis = glomerulus).

group of these organs a compact primitive kidney is formed, the anterior group taking part in the construction of the sexual organs.

In the more simple form that remains

throughout life. In the Myxinoidea and partly in the Selachii we find the primitive kidney first developing in the embryo of man and the higher Craniota (Figs. 386, 387). Of the two parts that compose the comb-shaped primitive kidney the longitudinal channel, or nephroduct, is always the first to appear; afterwards the transverse "canals," the excreting nephridia, are formed in the mesoderm; and after this again the Malpighian capsules with their tubular cells are associated with them as coelous outgrowths. The primitive renal duct, which appears first, is found in all craniate embryos at the early stage in which the differentiation of the midgut tube takes place in the ectoderm, the separation of the chorda from the visceral layer in the endoderm, and the first trace of the coelom-pouches arises between the limiting layers (Fig. 386). The nephroduct (*nud.*) is soon on each side, directly under the horny plate, in the shape of a long, thin, thread-like string of cells. It presently hollowes out and becomes a canal, running straight down from its birth, and clearly showing in the transverse section of the embryo its original position—the space between horny plate (*A*), primitive segments (*anv.*), and lateral plates (*apl.*). As the originally very short urinary canals lengthen and multiply, each of the two primitive kidneys assumes the form of a half-twisted leaf (Fig. 387). The lines of the leaf are represented by the urinary canals (*w.*), and the rib by the underlying nephroduct (*ad.*). At the lower edge of the primitive kidneys the rudiment of the ventral sexual gland (*g.*) can now be seen as a body of some size. The hindmost end of the nephroduct opens right behind into the last section of the rectum, thus making a cloaca of it. However, this opening of the nephroduct into the intestine must be regarded as a secondary formation. Originally they open, as the Cyclostomes clearly show, quite independently of the gut, in the extenal skin of the abdomen.

In the Myxinoidea the primitive kidneys retain this simple comb-shaped structure,

and a part of it is preserved in the Selachii; but in all the other Craniota it is only found for a short time in the embryo, as an autogenetic reproduction of the earlier phylogenetic structure. In these the primitive kidney soon assumes the form (by the rapid growth, lengthening, increasing, and narrowing of the urinary canals) of a large compact gland, of a long, oval or spindle-shaped character, which passes through the greater part of the azygous body-cavity (Figs. 183 et seqq., 388). It lies near the middle line, dorsally under the primitive vertebral column, and reaches from the cardiac



*Lamprey embryo, ventral view, showing the early stage of development before the formation of the azygous body-cavity, a prominent heart, a prominent liver, a large Malpighian system of glands, a Malpighian tubule, a portion of the digestive tract (intestine), a cloacal duct. (From Haeckel.)*

region to the cloaca. The right and left kidneys are parallel to each other, quite close together, and only separated by the mesentery—the thin narrow layer that attaches the middle gut to the under-surface of the vertebral column. The passage of each primitive kidney, the nephroduct, runs towards the back on the lower and outer side of the gland, and opens in the cloaca, close to the opening-point of the allantois; it afterwards opens into the allantois itself.

The primitive or primordial kidneys of the craniate embryo were formerly called the "Waldmeier bodies," and sometimes "Oliver's bodies." They act for a time as

kidneys, absorbing unusable wastes from the embryonic body and conducting them to the cloaca—afterwards to the allantois. There the primitive urine accumulates, and thus the allantois acts as bladder or urinary sac in the embryo of man and the other Amniotes. It has, however, no genetic connection with the primitive kidneys, but is a pouch-like growth from the anterior wall of the rectum (Fig. 247 a). Thus it is a product of the viscerotid layer, whereas the primitive kidneys are a product of the mesoblast layer. They

remain wall. It is true that many of the fishes also have a "bladder," but this is merely a local enlargement of the lower section of the nephroducts, and so totally different in origin and composition from the real bladder. The two structures can be compared from the physiological point of view, and so are analogous, as they have the same function; but not from the morphological point of view, and are therefore not homologous. The false bladder of the fishes is a mesodermic product of the nephroducts; the true bladder of the Dipneusts, Amphibia, and Amniotes is an epidermic blind sac of the rectum.

In all the Anamnia (the lower arthropods, the Ciliata, Cyclostomes, Pisces, Dipneusts and Amphibia) the urinary organs remain at a lower stage of development to this extent, that the primitive kidneys (protoxenophils) act per-

manently. This is only so as a passing phase of the early embryonic life in the three higher classes of Vertebrates, the Amniotes. In . . . the permanent or after-life (really the kidneys from nephridia) th

there appearance. They represent the adult and the graft of the

larval kidneys. The permanent kidneys do not arise (as was long supposed) as independent glands from the alimentary tube, but from the last section of the primitive kidneys and the nephroduct. Here a simple tube, the secondary renal duct, develops, near the point of its entry into the cloaca, and this tube grows considerably forward. With its blind upper or anterior end is connected a glandular sexual growth, that owes its origin to a differentiation of the last part of the primitive kidneys. This rudiment of the



FIG. 247a.

FIG. 247b.

FIG. 247c.

*Figs. 247a-c.—Primary and sexual organs of an embryo. Fig. 247a. Fish embryo one and a half weeks old. Fig. 247b. Fish embryo two and a half weeks old. Fig. 247c. Fish embryo three and a half weeks old. The W-shaped sac is the cloaca; that is followed by the rectum of more advanced fish; the lower and deeper part of which consists of a sac called the allantois; a layer of connective tissue surrounds the rectum and allantois. W-shaped sac is the cloaca; that is followed by the rectum of more advanced fish; the lower and deeper part of which consists of a sac called the allantois; a layer of connective tissue surrounds the rectum and allantois. (See text, v. Shallow, a modified theory.) (From Shallow.)*

hypothetically we must suppose that the allantois originated as a pouch-like growth from the cloaca-wall in consequence of the separation caused by the urine accumulated in it and excreted by the kidneys. It is originally a blind sac of the rectum. The real bladder of the vertebrate certainly made its first appearance among the Dipneusts (in Lepidostomias), and has been transmitted from bibia, and from these in the embryo of the latter it protrudes far out of the not yet closed

larval kidneys. The permanent kidneys do not arise (as was long supposed) as independent glands from the alimentary tube, but from the last section of the primitive kidneys and the nephroduct. Here a simple tube, the secondary renal duct, develops, near the point of its entry into the cloaca, and this tube grows considerably forward. With its blind upper or anterior end is connected a glandular sexual growth, that owes its origin to a differentiation of the last part of the primitive kidneys. This rudiment of the

permanent kidneys consist of coiled urinary canals with Malpighian capsules and vascular cells (without distinct funnels), of the same structure as the segmental metanephridia of the primitive kidneys. The further growth of these metanephridia gives rise to the compact permanent kidneys, which have the familiar bean-shape in man and most of the higher mammals, but consist of a number of separate folds in the lower mammals, birds, and reptiles. In the permanent kidneys grow rapidly and advance forward, their passage, sheath-like, detaches altogether from its birth-place, the posterior end of the nephroduct; it passes to the anterior surface of the allantois. At first in the adult Amniotes this ureter opens into the cloaca together with the last section of the nephroduct, but afterwards separates from this, and finally into the permanent bladder apart from the rectum altogether. The bladder originates from the middlemost and lowest part of the allantoic pedicle (vesicula), which enlarges in spindle shape before the entry into the cloaca. The anterior or upper part of the pedicle, which runs to the rectum in the ventral wall of the embryo, atrophies sufficiently, and only a number of epithelial cells of it is left as a rudimentary organ; that is the single recto-allantoic ligament. To the right and left of it in the adult man are a couple of other rudimentary organs, the lateral vesicumbilical ligaments. These are the degenerate string-like ruffles of the earlier umbilical arteries.

Though in man and all the other Amniotes the primitive kidneys are thus early replaced by the permanent kidneys, and these alone then act as urinary organs, all the parts of the former are by no means lost. The nephroduct becomes very important physiologically by being converted into the passageway of the sexual glands. In all the Crustaceans—or all the Vertebrates from the fishes up to man—a second similar canal develops beside the nephroduct at an early stage of embryonic evolution. The latter is usually called the Müllerian duct, after its discoverer, Johannes Müller, while the former is called the Wolffian duct. The origin of the Müllerian duct is still obscure; comparative anatomy and embryology seem to indicate that it originates by differentiation from the Wolffian duct. Perhaps it would be best to say:—The

original primary nephroduct divides by differentiation (or longitudinal cleavage) into two secondary nephroducts, the Wolffian and the Müllerian ducts.<sup>1</sup> The latter (Fig. 379 a) lies just on the inner side of the former (Fig. 379 b). Both open behind into the cloaca.

However uncertain the origin of the nephroduct and its two products, the Müllerian and the Wolffian ducts, may be, its later development is clear enough. In all the Crustaceans the Wolffian duct is converted into the spermiduct, and the Müllerian duct into the oviduct. Only one of these is retained in each sex; the other either disappears altogether, or only leaves traces in the shape of rudimentary organs. In the male sex,



FIG. 379.—Primary sexual organs of a female Crustacean. (After E. G. P. H. von Reichenbach.) a, Müllerian duct; b, Wolffian duct; c, oviduct; d, spermiduct; e, recto-allantoic ligament. (See also Fig. 394.)

in which the two Wolffian ducts become the spermiducts, we often find traces of the Müllerian ducts, which I have called "Rudber's canals" (Fig. 394 c). In the female sex, in which the two Müllerian ducts form the oviducts, there are cells of the Wolffian ducts, which are called "the ducts of Gaertner."

We obtain the most interesting information with regard to this remarkable evolution of the nephroducts and their association with the sexual glands from the Amphibia (Figs. 390–395). The first structure of the nephroduct and its differentiation into Müllerian and Wolffian ducts are just the same in both sexes in the Amphibia, as in the mammal embryos (Figs. 392, 393). In the female Amphibia

the Mullerian duct develops on either side into a large oviduct (Fig. 393 a), while the Wolffian duct acts permanently as ureter (w). In the male Amphibia the Mullerian duct only remains as a



FIG. 393.—Original position of the sexual ducts in the ventral cavity of the embryo. The Mullerian ducts (m) are shown as separate ducts, opening into the cloaca (c); the Wolffian ducts (w) are shown as separate ducts, opening into the cloaca (c). The gonads (g) are shown as small ovoid bodies, situated in front of the kidneys. The cloaca (c) is shown as a large cavity, containing the rectum, the bladder, and the openings of the kidneys, the rectum, the bladder, and the rectum.

rudimentary organ without any functional significance, as Rathke's canal (Fig. 394 c), the Wolffian duct serves also as ureter, but at the same time as spermatoduct, the spermatocauda (sc) that proceed from the testicles (t) emerging the fore part of the primitive kidneys and joining them with the urinary can-

In the mammals these pre-amphibian features are only seen as brief phase of the earlier period of embryonic development (Fig. 395). Here the primitive kidneys, which act as excretory organs of urine throughout life in the amniote-less Vertebrates, are replaced in the mammals by the permanent kidneys. The real primitive kidneys disappear for the most part at an early stage of develop-

ment, and only small relics of them remain. In the male mammal the epididymis develops from the uppermost part of the primitive kidney; in the female a useless rudimentary organ, the epoophoron, is formed from the same part. The streptiodial relic of the former is known as the parotidkidney, that of the latter as the parotis.

The Mullerian duct undergoes very important changes in the female mam-

mals; proper are developed only their upper part; the lower part elongates into a spindle-shaped tube with a lumen, in which the im-  
pugnated ovum develops in boys. That is the womb (*uterus*). At first the two womb (Fig. 395 a) are completely separate, and open into the cloaca on either side of the bladder (bl), as is still the case in the lowest living mammals, the Monotremata. But in the Marsupials a communication is opened between the two Mullerian ducts, and in the Placentalia they combine below with the rudimentary Wolffian ducts to form a single "genital canal." The original independence of the two ovaries and the vaginal canals formed from their lower ends are retained in many of the lower Placentals, but in the higher they gradually blend and form a single organ. The conjunction proceeds from below (or behind) upwards (or forwards) in many of the Rodents (such as the rabbit and squirrel) to a separate womb still open into the simple and single vaginal canal, but in others, and in the Carnivora, Cetacea, and Ungulates, the

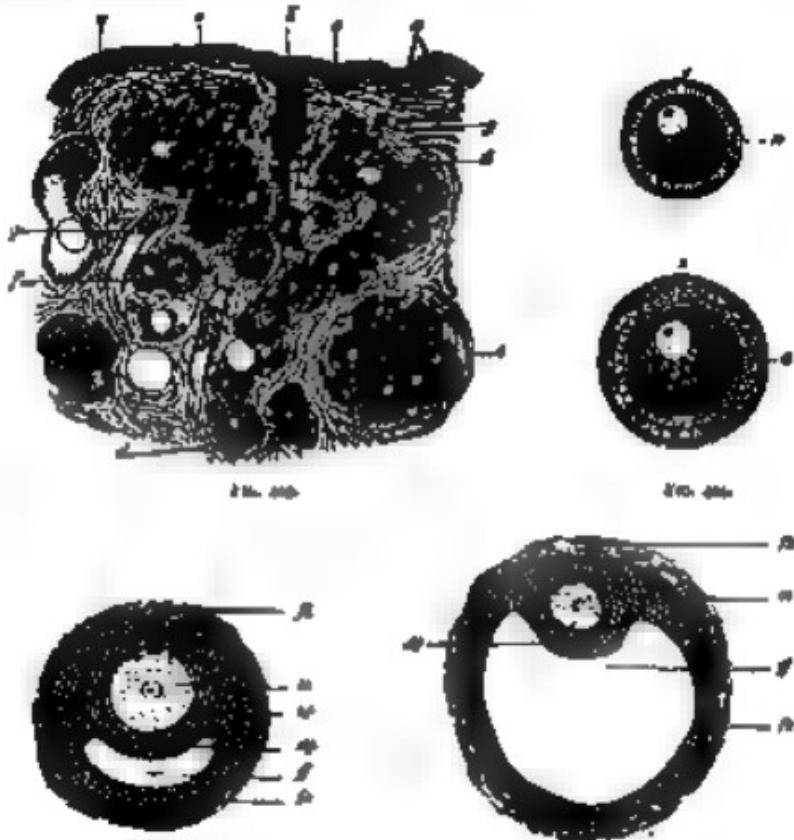


FIG. 395.—Diagrammatic sketch of a frog's genital system in front, double viewed in a median section, 20 mm. A median section, 20 mm.

lower lobes of the womb have already fused into a single piece, though the upper lobes (or "horns") are still separate ("two-horned" womb, *uterus bicarinatus*). In the bats and lemurs the "horns" are

very short, and the lower common part is longer. Finally, in the eyes and in man the blending of the two halves is complete, and there is only the one muscle.

of the Maldives



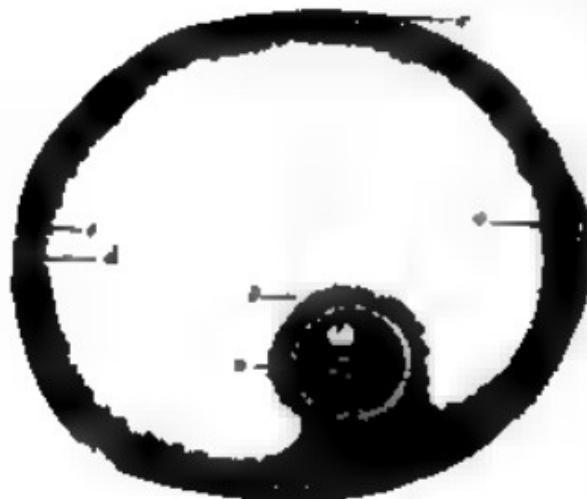
The eye-spot.—Origin of leaves over in the female ovary. For ex. Vertical section of the ovary of a two-month female where, a certain spot, a secondary growth of young ovules in the axils of long rows of ovules with fully-formed Ovule's (which is a group of 1-2 mm. long, yellowish, young folioles, of which each consists in successive lesser whorls) of the ovule. In the axiles the young ovules distinguished by their conspicuously fine filaments (Grafe, Wissner).

FIG. 46.—Two young *Ctenidium scutellatum*, ventral. In 1 the cuticle-cells still have a simple, and in 2 a double, margin round the plates at one, or 3 they are beginning to form the transverse, or the latero-lateral, fold.

For ages and ages—Two older Cyclospora infections, in which food is important to accumulate under the numerically increased epithelial mass of the intestinal lining, engorged with blood, and with much cellular debris; so the young ova, with their young transformed eggs, of course, or some germs, will become proliferate, formed in the body, which surround the young, full-fledged, former, cellular, a granulated mass, about 1/8 & 1/4 millimeters diameter. During growth of the intestinal epithelia (these millions).

pear-shaped uterine pouch, into which the oviducts open on each side. This simple uterus is a late evolutionary stage at their lower ends. Here again they form a single genital cord (Fig. 107c), and this opens similarly into the

original urogenital sinus, which develops from the lowest section of the bladder (2). But while in the male mammals the Wolffian ducts develop into the permanent spermatocysts, there are only rudimentary relics left of the Müllerian ducts. The most notable of these is the "male uterus" (*utriculus masculinus*), which originates from the lowest fused part of the ducts, and corresponds to the female uterus. It is a small, flask-shaped vesicle without any physiological significance, which opens into the ureter between the two spermatocysts and the prostate (the *vesicula prostatica*).



*—A State Supreme Court Justice, at the opening session of the Legislature, / Soothed the apprehensions of the people, by the words,*

The internal sexual organs of the mammals undergo very distinctive changes of position. At first the gonadoid glands of both sexes lie deep within the ventral cavity, at the inner edge of the primitive kidneys (Figs. 316 A, 320 A), attached to the vertebral column by a short mesentery (*mesonephros* in the male, *metonephros* in the female). But this primary arrangement is retained permanently only in the Monotremes (and the lower *Vertebrates*). In all other mammals (both *Marsupials* and *Placental*s) they leave their cradle and travel more or less — — — (or behind), following the direction of a segment that goes from the primitive

kidneys to the inguinal region of the ventral wall. This is the inguinal ligament of the primitive kidneys, known in the male as the Hunterian ligament (Fig. 400 6d), and in the female as the "round maternal ligament" (Fig. 401 2). In women the ovaries travel more or less towards the small pelvis, or enter into it altogether. In the male the testicles pass out of the ventral cavity, and penetrate by the inguinal canal into a sac-shaped fold of the outer skin. When the right and left folds ("scrotal evaginations") join together they form the scrotum. The various mammals bring before us the successive stages of this displacement. In the elephant and the whale the testicles descend very little, and remain underneath the kidneys. In many of the rodents and carnivores they enter the inguinal canal. In most of the bigger mammals they pass through this into the scrotum. As a rule, the inguinal canal closes up. When males open the scrotum periodically (as the scrotum withdraws into the cavity again) of rat ("—") — (pigs, rodents, bats, etc.).

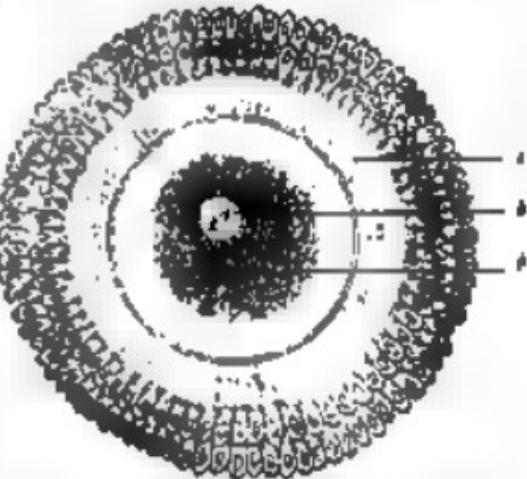
The structure of the external sexual organs, the copulatory organs that convey the fecundating sperm from the male to the female organism in the act of copulation, is also peculiar to the mammals. There are no organs of this character in most of the other Vertebrates. In those that live in water (such as the Acrania and Cyclostomes, and most of the fishes) the ova and sperm-cells are simply ejected into the water, where their conjunction and fertilisation are left to chance. But in many of the fishes and amphibia, which are viviparous, there is a direct conveyance of the male sperm into the female body; and this is the case with all the Amniotes (reptiles, birds, and man). In these the urinary and sexual ducts always open originally into the last of the rectum, which thus forms a cloaca.

(p. 349). Among the mammals this arrangement is permanent only in the Monotremes, which take their name from it (Fig. 359 *et seq.*). In all the other mammals a frontal partition is developed in the cloaca (in the human embryo about the beginning of the third month), and this divides it into two cavities. The anterior cavity receives the urino-genital canal, and is the ante- outlet of the uterus and the sexual products; the hind or anus-cavity passes the excretions only.

Even before this partition has been formed in the Mammals and Pterosaurs, we see the first trace of the external sexual organ. First a conical protuberance rises at the anterior border of the cloaca-cutlet—the sexual prominence (*phallus*, Fig. 402 A, c, B, e). At the tip it is swollen in the shape of a club ("acorn" phallus). On its under side there is a furrow, the sexual groove (*furculus genitale*, f), and on each side of this a fold of skin, the "sexual fold" (*flammeopunctata*, g / ). The sexual protuberance or phallus is the chief organ of the sexual sense (spile); the sexual nerves spread on it, and these are the principal organs of the specific sexual irritation. As schools (adults / herds / herds / ) are developed in the male phallus by peculiar modifications of the blood-vessels, it becomes capable of extracting periodically a strong excretion of blood, becoming stiff, so as to penetrate into the female vagina under this effect copulation to the male the phallus becomes the penis; in the female it becomes the much smaller clitoris; this is only found to be very large in certain species (*Apteronotus*). A prepuce ("flammeo-skin") is developed in both sexes as a protecting fold on the anterior surface of the phallus.

The external sexual member (*phallus*) is found at various stages of development within the mammal class, both in regard to size and shape, and the differentiation and structure of its various parts; this applies especially to the terminal part of

the phallus, the glans, both the larger glans process of the male and the smaller glans discolor of the female. The part of the cloaca from the upper wall of which it forms belongs to the proctodaeum, the ectodermic invagination of the rectum (p. 312); hence its epithelial covering can develop the same horny growths as the cutaneous layer of the epidermis. Thus the glans, which is quite smooth in man and the higher apes, is covered with spines in many of the lower apes and in the cat, and in many of the rodents with hairs (marmot) or scales (guinea-pig) or



The age.—The larvae were yellow after hatching from the Ootheca, followed immediately by the change into the first instar larva (in 100 individuals examined) and were pale yellowish-green, with reddish posterior margin, a distinct dorsal longitudinal line, and a dark brown, irregular, higher ventral line, a median line of the same (hypopygial vesicle). Of these younger, unengorged specimens (100% yellow), 20% were 0.5 mm. long, 10% 0.6 mm., 20% 0.7 mm., 20% 0.8 mm., 20% 0.9 mm., 10% 1.0 mm., and 10% 1.1 mm.

solid horny whets (flesher). Many of the Ungulates have a free conical projection on the glans, and in many of the *Ruminantia* this "phallus-tentacle" grows into a long cone, bent hook-wise at the base (as in the goat, antelope, gnu, etc.). The different forms of the phallus are connected with variations in the structure and distribution of the sensory corpuscles—i.e., the real organs of the sexual sense, which develop in certain parts of the corium of the phallus, and have been evolved from ordinary tactile corpuscles of the corium by specific adaptation (see *vide*).

The formation of the corpus cavernosum, which gives the stiffness of the phallus and its capability of supporting the weight, by certain special structures of this spongy vascular system, also shows a good deal of variety within the vertebrates. This stiffness is increased by many efforts of mammals (especially the apes and monkeys) by the contraction of a part of the fibrous wall of corpus cavernosum. This production (or pumping) is very large in the hedgehog and deer, and less than a tenth in the mouse; it is also very large in some of the lower apes, and proportionate to that in the gibbon. It is greatest in man of the anthropoid apes; it seems to have been lost in chimpzee (and in man) by atrophy.

The sexual glands on the under side of the phallus remain in the male the result of the unpaired sexual, and in females make a sacculus or sheath, containing a closed canal by the posterior of its parallel edges, the male urethra. In the female the only later phase is a few cases (some of the lemurs, rhesus, and marmoset), at a rate, the glands remain open, and the borders of this "vestibule of the urethra" develop into the vesicle (hypopygium). The large lobes of the female develop from the paired parts (two gonads); the two rounded lobes of the sheath that are fused at each side of the genital groove. They join together in the male, and form the closed urethra. These striking differences between the two main courses just described is the human embryo at the ninth week. We begin to trace them to the tenth week of development, and they are incorporated in proportion to the difference of the sexes developed.

Between the normal function of the two sexual parts in the male fails to take place, and the sexual glands may also remain open (hypopygium). In these cases the external male glands resemble the female, and they are often strongly regarded as case of hermaphroditism. Other malformations of various kinds are not infrequently found in the human external sexual organs, and some of them have a good morphological interest. The reverse of hypopygium, in which the penis is split open below, is man in hypopygia, in which the urethra is open above. In this case the corporal sinus opens above at the dorsal end of the penis; in the former case down below. There are similar malformations interesting

with a man's generative power, and they predominantly affect his sexual development. They clearly prove that potency is not granted by a "Sexual Proteins," but left to the play of blind chance.

We must carefully distinguish the rarer cases of real hermaphrodites from the pseudogenes. This is easily found when the principal organs of reproduction, the genital glands of both sexes, are united in one individual. In these cases either an ovary is developed on the right and a testis on the left (or vice versa); or else there are testicles and ovaries on both sides, some more and others less developed. As hermaphrodites were probably the original arrangement in all the Vertebrates, and the division of the sexes only followed by later differentiation of these, these varieties cases affect the development differently. But they are rarely found in man and the higher mammals. On the other hand, we constantly find the original hermaphroditism in some of the lower Vertebrates, such as the *Myrophis*, many kinds of the *Perichthys* (*carpoides*), and some of the *Ampelisca* (eel-like, eels). In these cases the male often has a rudimentary ovary in the fore and in the testicle; and the female sometimes has a rudimentary, inactive testicle. In the carp also and some other fishes this is found occasionally. We have already seen how traces of the earlier hermaphroditism may be traced at the junctions of the Amphibia.

Man has definitely preserved the main features of his masculinity in the majority of his sensory and sexual organs. We can follow their development step by step in the human embryo in the same advancing gradation that is presented to us by the comparison of the unpaired organs in the *Arculus*, *Cyclostomes*, *Fishes*, *Amphibia*, *Reptiles*, and the *Mammals* (in several series) in the *Mollusca*, *Starfishes*, and the *Crustaceans*. All the particularities of vertebrate structures that distinguish the mammals from the rest of the Vertebrates are found in man; and in all species throughout Nature he resembles the apes, particularly the anthropoid apes. In view of the fact that the specific features of the primates have been inherited by man, I will, in conclusion, point out the unusual way in which the sex are formed in the ovary. In all the mammals the ovaries are contained in special capsules, which are fixed on the Ovarian

follicles after their discovery, Ringer de Graaf (1677). They were formerly supposed to be the ova themselves; but later discovered the ova within the follicles (p. 16). Each follicle (Fig. 409) consists of a round fibrous capsule (*a*), which contains fluid and is lined with several strata of cells (*b*). The layer is thickened like a knob at one point (*c*); this ovum-capsule encloses the ovum proper (*d*). The mammal ovary is originally a very simple oval body (Fig. 397 *a*), formed only of connective tissue and blood-vessels, covered with a layer of cells, the ovarian epithelium or the female germ epithelium. From this germ epithelium sprouts of cells grow out into the connective tissue or "stroma" of the ovary (Fig. 402 *b*). Some of the cells of these sprouts (or Pflüger's tubes) grow larger and become ova (primitive ova, *c*), but the great majority remain small, and form a protective and nutritive stratum of cells round each ovum—the "follicle-epithelium" (*d*).

The Follicle-epithelium of the mammal has at first one stratum (Fig. 402 *d*), but afterwards several (*e*). It is true that in all the other Vertebrates the ova are enclosed in a membrane, or "follicle," that consists of smaller cells. But it is only in the mammals that fluid accumulates between the growing follicle-cells, and distends the follicle into a large round capsule, on the inside wall of which the ovum lies, at one side (Figs. 405, 406). That again, as in the whole of his morphology, man proves indubitably his descent from the mammals.

In the lower Vertebrates the formation of ova in the germ-epithelium of the ovary continues throughout life; but in the higher it is restricted to the earlier stages, or ova to the period of embryonic develop-

ment. In man it seems to cease in the first year; in the second year we find no new-formed ova or chains of ova (Pflüger's tubes). However, the number of ova in the two ovaries is very large in the young girl; there are calculated to be 72,000 in the sexually-mature maiden. In the production of the ova man resembles most of the anthropoid apes.

Generally speaking, the natural history of the human sexual organs is one of those parts of anthropology that furnish the most convincing proofs of the animal origin of the human race. Any man who is acquainted with the facts and impartially weighs them will conclude from them alone that we have been evolved from the lower Vertebrates. The larger and the detailed structures, the action, and the embryological development of the sexual organs are just the same in man as in the apes. This applies equally to the male and the female, the internal and the external organs. The differences we find to this respect between men and the anthropoid apes are much slighter than the differences between the various species of apes. But all the apes have certainly a common origin, and have been evolved from a long-extinct early-Tertiary stem-form, which we must trace to a branch of the lemurs. If we had this unknown pithecoid somewhere before us, we should certainly put it in the order of the true apes in the primate system; but within this order we cannot, for the anatomical and ontogenetic reasons we have seen, separate man from the group of the anthropoid apes. Here again, therefore, on the ground of the pithecomimetic principle, comparative anatomy and ontogeny teach with full confidence the descent of man from the apes.

## CHAPTER XXX.

### RESULTS OF ANTHROPOGENY

Now that we have traversed the wonderful region of human embryology and are familiar with the principal parts of it, it will be well to look back on the way we have come, and forward to the further path to truth to which it has led us. We started from the simplest form of embryo, or the development of the individual, from observations that we can repeat and verify by microscopic and anatomical study at any moment. The first and most important of these facts is that in every man, like every other animal, begins his existence as a single cell. This round cell has the same characteristic form and origin as the ovum of any other mammal. From it is developed, in the same manner in all the Placentalia, by repeated cleavage, a multicellular blastula. This is converted into a gastrula, and this in turn into a blastocyst (or embryonic vesicle). The two units of cells that compose the wall are the primary germinal layers, the skin-layer (ectoderm), and gut-layer (endoderm). The two-layered embryonic form is the ontogenetic reproduction of the extremely important phylogenetic stem-form of all the Metazoa, which we have called the Gastraea. As the human embryo passes through the gastrula-stage (as that of all the other Metazoa), we also trace its phylogenetic origin to the Gastraea.

As we continued to follow the embryonic development of the two-layered structure, we saw that first a third, or middle layer (mesoderm), appears between the two primary layers; when this divides into two, we have the four secondary germinal layers. These have just the same composition and genetic significance in man as in all the other Vertebrates. From the skin-series layer are developed the epidermis, the central nervous system, and the chief part of the sense-organs. The skin-fibre layer forms the connective and the motor organs—the skeleton and the muscular system. From the gut-fibre layer are developed the vascular system, the muscular wall of the gut, and the sexual glands. Finally, the uncolored

layer only forms the epithelium, or the finer cellular stratum of the mucous membrane of the alimentary canal and glands (liver, etc.).

The manner in which these different systems of organs arise from the mediodorsal germinal layers is essentially the same from the start in man as in all the other Vertebrates. We see, in studying the embryonic development of such organs, that the human embryo follows the special laws of differentiation and separation that are only found elsewhere in the Vertebrates. Within the limits of this vast stem we have followed, step by step, the development both of the body as a whole and of its various parts. This higher development follows in the human embryo the form that is peculiar to the mammals. Finally, we see that, even within the limits of this class, the various phylogenetic stages that we distinguish in a natural classification of the mammals correspond to the ontogenetic stages that the human embryo passes through in the course of its evolution. We are thus in a position to determine precisely the position of man in this class, and so to establish his relationship to the different orders of mammals.

The line of argument we followed in this explanation of the ontogenetic data was nothing but a consistent application of the biogenetic law. In this we have throughout taken strict account of the distinction between palingenetic and ontogenetic phenomena. Palingenesis (or "synthetic development") alone enables us to draw conclusions from the observed embryonic form to the adult-form preserved by heredity. Such inference becomes more or less precarious when there has been conjugation, or disturbance of development, owing to fresh adaptations. We cannot understand embryonic development unless we appreciate this very important distinction. Here we stand at the very limit that separates the older and the new science or philosophy of nature. The whole of the results of recent monstrosity research cannot be irresistibly

To complete the biological law and to strengthen communism. These are, it is true, irreconcilable with the biological and doctrinal of former days, that have been maintained on us by religious education. But without the dispensing law without the distinction between permanence and corruption, and without the theory of evolution on which we base it, it is quite impossible to understand the laws of organic development—without them we cannot cast the former gloses of explanation over this theoretical field of phenomena. But when we recognize the causal connection of anatomy and physiology expressed in this law, the broader parts of pathology are susceptible of a very simple explanation; they are found to be the necessary and natural effects of the evolution of the mass, determined by the laws of heredity and adaptation. The corrective action of these laws under the natural influence of the struggle for existence, or vice versa may be a word, Mr. Darwin's "natural selection," is entirely adequate to explain the whole process of embryology in the light of evolution. It is the chief merit of Darwin that he replaced by his theory of selection the correlation of the laws of heredity and adaptation that Lamarck had recognized, and passed over the tree may be much a sound interpretation of evolution.

The phenomenon that it is more important to recognize in this connection is the significance of functional variations. Jean Lamarck was the first to appreciate its fundamental importance in this, and as they themselves readily give the name of Lamarckian to the theory of descent he based on it. Hence the radical opponents of the latter have very properly denied their authorship chiefly against the former. One of the most distinguished and most adverse students of these oppositions, Mr. John H. Evans, writes very profitably that "correspondences observed in the life of the individual are not hereditary."

The inheritance of acquired characters is denied, not only by thorough opponents of evolution, but even by advocates who admit it and have maintained a position in the establishment, especially Westcott, Collier, Ray Lanier, etc. Oliver Ladd, the chief opponent has been August Weismann, who has denied the functionaries in the development of Darwin's theory of descent. In his book on *The Ontogeny of the Germ-*

*plasm*, and in his recent excellent *Lectures on the Theory of Descent* (1897), he has with great success advanced the opinion that "only those characters can be inherited as transmissible, that were manifested in reproductory form in the parents." However, this genealogical theory, such as attempts to explain heredity in merely a "preliminary" manner, is in one of three metaphysical speculations that exclude the evolutionary phenomena, exclusive to learned men, and regard the influence of the pernicious as insignificant. Herbert Spencer, Thomas Huxley, Lester Ward, Huxley, and Zamenhof have pointed out the *unconscious consequences* of this position. I have given my view of it in the conclusion of the *Mystery of Creation* (pp. 194, 202). I hold, with Compton and others, that the hereditary transmission of acquired characters is one of the most important phenomena in biology, and is proved by thousands of morphological and physiological experiments. It is an indispensable foundation of the theory of evolution.

Of the many and weighty arguments for the truth of this conception of evolution I wish for the reader briefly refer to the analogous evidence of dysmorphology, the science of rudimentary organs. We cannot doubt the value of the authority on the great physiological significance of these remarkable organs, which are now plainly visible from the physiological point of view. We find some of these rudimentary parts, isolated from the more developed, a number, in every system of organs, and will be higher structures. Thus we find at once on the skin a variety and rudimentary web of hair, only fully developed on the head, under the eyebrows, and at a few other parts of the body. The skin hairs are the greater part of the body are quite useless and devoid of physiological value, they are the last relic of the older hairy race of our simian ancestors. The mimic appendages furnish a series of most remarkable rudimentary organs. We have seen that the whole of the skin of the external ear, with its cartilage, muscle, and skin, is at one a mimic appendage, and has not the physiological importance that we formerly ascribed to it. It is the deeper convolutions of the mind, body, soul, and man, the number of which we can hardly count well there. We find also

lower strata of our age—a small, median, mandibular fold that is of no use whatever to us, and is only interesting as the last trace of the retreating mandible, that had, I may add, had a distinct physiological purpose in the animal stage, and still has in many of the Apes.

The motor apparatus, in both the digestive and respiratory systems, provides a number of interesting embryological experiments. I need only recall the preceding tail of the human embryo, which is rudimentary caudal vertebrae and muscles; this is usually useless in man, but very interesting as the degeneration of the long tail of the simian ancestors. From these we have also inherited various busy processes and organs, which were very useful in childhood, but are useless to us at various points of life as we have extensive muscles which are never incapable of a strongly-developed caudal muscle in our lower mammal ancestors. This "pancreaticus caudatus" had the function of extracting and carrying the salts to those areas the skin, as we use every day in the home. Another point of one of his large caudal organs is in the frontal sinuses, by which we took our breath and saw our eye-tears. But there is another considerable relic of the large caudal organs in the nose ("nasus appendicis"), over which we have no voluntary control.

Not only in the systems of animal regions, but also in the vegetal apparatus, we find a number of rudimentary organs, many of which we have already noticed. In the alimentary apparatus there are the thyroids-gland and the thyroid gland, the root of guttae and the roots of a fibrous growth that the Tunicates and Ascidia still have in the gill-pores; there is also the cornua-like appendix to the oesophagus. In the vascular system we have a number of useless veins which represent relics of atrophied vessels that are now active in birds—such as the ducts between the pulmonary artery and the aorta, the shunt vessels between the portal vein and the hepatic veins, and many others. The many rudimentary organs in the urinary and sexual apparatus are particularly interesting. There are generally developed in man and rudimentary in the other. Thus the epididymis are formed from the Malpighian ducts in the male, whereas in the female we have merely rudimentary

traces of them in Cetacean's bladders. On the other hand, in the female the ovaries and womb are developed from the Malpighian ducts, while in the male only the lowest coils of them, known as the "male womb" (ovario-pandictus). Again, the male has in his nipples and mammary glands the rudiments of organs that are usually active only in the female.

A careful anatomical study of the human frame would dictate as to numbers of other rudimentary organs, and these can only be explained on the theory of evolution. Robert Whistler has collected a large number of them in his work on *The Human Frame as a Museum of Man*. They are some of the singular proofs of the truth of the mechanical hypothesis and the strengthen argument of the educational type. If on the same demand, just as we see other organs have been designed and fitted for the purpose from the start and brought into being by a creative act, the existence of these rudimentary organs would be an insurmountable objection. It would be impossible to understand why the Creator had put this useless burden on his creature to walk a path that is in itself so devoid of beauty. But the theory of evolution gives the simplest possible explanation of them. It says, The rudimentary organs are parts of the body that have fallen away in the course of evolution, they had definite functions in our animal ancestors, but have lost their physiological importance. On account of such importance they have become important, but are transferred from generation to generation by heredity, and gradually strengthened.

We have isolated out only three rudimentary parts, but all the organs of the body, from the momentary—protemporally from the eggs. The human body does not contain a single organ that has not been isolated from the eggs. In fact, with the aid of our binoculars how we can trace the origin of our various species of organs much further, down to the lowest stages of our ancestry. We may say, for instance, that we have inherited the oldest organs of the body, the external skin and the internal part of the alimentary system, from the Cetaceans; the nervous and muscular systems from the Piscines; the reproductive, the body-cavity, and blood from the Vertebrates; the glands and the blood vessels from the Prothoracians;

the articulation of the body from the head; the primitive skull and the higher brain-organs from the Cyclostomes; the body and liver from the Fishes; the fore-limb from the Amphibia; the pelvis from the Reptiles; the hairy coat, the mammary glands, and the external sexual organs from the Primates. When we determined "the law of the homoplastic connection of apparently related forms," and determined the relative age of organs, we now know it was possible to draw phylogenetic conclusions from the homoplastic connection of systems of organs.

With the aid of this important law and of comparative anatomy we were also enabled to determine "man's place in nature," or, as we put it, enough to make positive at the classification of the animal kingdom. In some morphological characters the animal world is divided into twelve series of groups, and these are usually distributed over about sixty classes, and these classes are of four orders. In his three organisms man is most especially, at the first place, a member of one of these series, the vertebrate group; secondly, a member of one particular class of this group, the Mammals, and thirdly, of one particular order, the order of Primates. He has all the characteristics that distinguish the Vertebrates from the other class of animal series, the Molluscs from the other early classes, and the Crustaceans from the yet other orders of the animal kingdom. We may have had to sit on the floor, but we cannot go over the fact of connection and classification. Of late years the fact has often risen to a good deal of discussion, and especially of controversy as to the particular systematic relationship of man to the apes. The most serious opinion has been advanced on this "ape-man," or "pithecoid-theory." It is no odd, therefore, to go into it more fully and distinguish the material from the nominal. (K. *cit.* p. 26-5.)

We start from the well-known fact that man is in very case—whether we accept or reject his special blood relationship to the apes—a little ancestral; or, fact, a pleiotomous. This fundamental fact can be proved so easily at any moment from comparative anatomy that it has been universally admitted since the opposition of the Phrenologists from the lower mammals (Therapsidae and Monotremes). But for very evident rea-

son to the theory of evolution it must follow at once that man derives from a common ancestor with all the other Primates, the common ancestor of the Primates, just as we must admit a common progenitor ancestor of all the mammals. This is, however, to settle definitely the great and moving question of man's place in nature, whether or no we go on to admit a nearer or more distant relationship to the apes. Whether man is or is not a member of the order (or, if you prefer, the primate-order) in the phylogenetic sense, is in any case the direct link connecting to the rest of the mammals, and especially the Primates, as accomplished. It is possible that the addition of the various orders of mammals to each other are different from what we biogenetically assume today. But, in any case, the common descent of man and all the other mammals from one main-form is beyond question. This long-existent Primateform was probably evolved from Proteropithecus during the Tertiary period, and must necessarily be regarded as the nearest and earliest ancestor of all the mammals.

If we hold firmly to this fundamental and most important idea, we shall see the "ape-man" in a very different light than that in which it is usually regarded. Little reflection is then needed to see that it is not nearly so important as it is said to be. The origin of the human race from a series of numerous ancestors, and the biologic evolution of these from the earlier forms of lower vertebrate ancestors, together with all the weighty conclusion that every living being man included therein, comes unproved, or for us these are unproved. It is immaterial whether we regard this "ape" as our nearest ancestor or not, that as it has helped the factors to lay the chief stress in the whole question of man's origin on the closest form the apes. I am compelled to return to it, even here, and recall the fact of comparative anatomy and comparative physiology that give a decisive answer to the ape-question.

The shortest way to state our purpose is that followed by Huxley in 1863 in his well-known work, which I have already often quoted, *Huxley's Home in Nature*—the law of comparative anatomy and embryology. We have to compare biogenetically not only a species with the same organs in the higher apes, and then to compare it the difference between the two are greater

then the corresponding differences between the higher and the lower ages. The intellective and imaginative race of this comparative-sociology may be compared with the greater one and importance; and the physical anthropologist, which we have called the Hunterian age in honour of its foremost country, has the difference in importance between race and the most advanced ages we know are much slighter than the corresponding difference in importance between the higher and lower ages. We may even give a more precise formula to this law, by calling the Paleolithic or American ages as *discrete* relatives, and equating the importance to the narrower family-circle of the Caucasians, the ages of the Old World. Within the limits of this small group of mammals we find the structural differences between the lower and higher carnivorous ages—for instance, the baboon and the gorilla—to be much greater than the differences between the anthropoid ages and ours. If we now turn to compare, and find, according to our "law of the comparative generation of systematically related forms," that the embryo of the anthropoid ages and man made their revolutionised for a longer time than the embryo of the baboon and the lowest ages, we are forced, whether we like it or not, to recognise our descent from the lower of ages. We are naturally inclined to apprehend a picture of the transformation of the form of our early Tertiary ancestors from the surprising facts of comparative anatomy; however we may know this in detail, it will be the picture of a tree age, and a distinct carnivorous age. This has been shown so well by Flasby (ibid.) that the names which of Klemm, Viret, and other anthropologists, have completely failed (cf. pp. 327-328). All the structural characters that distinguish the Caucasians from the Americans are found in man. Hence in the genealogy of the savages we must derive our humanity from the carnivorous group, and locate the origin of the human race in the Old World. Only the early race from which both descended was common to them.

It is, therefore, established beyond question for all impartial intellective inquiry, that the human race comes directly from the ages of the Old World; but, on the same time, I repeat that this is not so important in connexion with the main

question of the origin of ages as is generally supposed. Even if we could fully prove it, in this case we have learned still the empirical fact of comparative anatomy and morphology as to the present-day character of these savages unmodified. These prove beyond all doubt the common descent of man and all the rest of the mammals. Further, the main question is not in this case affected if it is held: "It is true that man is a mammal, but he has developed at the very root of the stem from all the other mammals, and has no closer relationship to any living group of mammals." The validity of this or that claim in any case, if we examine the relation of the savages alone to the sixty other classes of the animal world. Quite certainly the whole of the mammals, including man, have had a common origin; and it is equally certain that their common fore-fathers were probably evolved from a long series of Lower Vertebrates.

The resistance to the theory of a descent from the ages is clearly due in most cases to feeling rather than to reason. They shrink from the notion of such an origin just because they see in the ages evolution a curiously slow, a diverted and unnatural history of development; because it depicts man's ancestry as placidity and half-inertness. It is often startling to think up how descended from some lofty and grandiose being; and we find the verdict there, because every has been induced to believe in our origin from gods or demigods. The Church, with that singular regard of man of which it is a master, has succeeded in representing the ridiculous place of vanity in "Christianity", and the very men who reject with horre the notion of an animal origin, and name themselves "children of God," love to pride of their "divine sons of men." In one of the sermons that have passed me these pugnacious and bitter against the doctrine of evolution become vanity and cannot have had a strengthened character; and, although we have learned the very clear truth, wherein from the ages we must admit that we have descended it to a higher degree, which is evidently represented by man and several hominoids. We are greatly assisted in all the obstinate fiction that the religious pride of antiquity has unmodified from the Middle Ages to the present time; yet there is a large amount of this empty fable in

most men. And we must supply much more to bring their family back to some approximate human or later human phase rather than to an animalistic process, so that man would rather have as part of the race a useful and kind Adam, than an advertising and vigorous Apes. It is a matter of time, and to this extent we cannot control over these preexisting differences. Presently, the amount of time is more important than that of descent. It seems to be a fact that in the advanced offspring of a single ancestor, that has developed progressively along the lower mammals in the struggle for life, than the degeneration demanded of a primitive being, results from a slow and halting bar to man, and as it originated from one of his ribs. Speaking of the ribs, I may add to what I have said about the development of the skeleton that the number of ribs is just the same in man and woman. In both of them the ribs are formed from the middle germinal layer, and are, from the physiological point of view, later or second vertebrae.

But it is odd: "That is all very well, as far as the human body is concerned; but the form quoted is so impossible to decide that it has really and gradually been evolved from the long ancestral series of the Vertebrates. But it is quite another thing as regards man's mind, as well; this cannot possibly have been developed from the vertebrates, and" Let us see if we cannot start this group without losing the connection here of comparative anatomy, physiology, and embryology. It will be best to begin with a comparative study of the minds of various groups of Vertebrates. Here we find over an enormous variety of vertebrate forms that, at first sight, is truly quite impossible to trace them all to a common "Primitive Vertebrate." Think of the tiny Amphisbaenians, which we find from but a simple mouth-and-toe, and no whole psychic life at the very lowest stage among the Vertebrates. The following group of the Cyclostomes are still very limited, though they have a brain. When we pass on to the fishes, we find their intelligence remaining at a very low level. We do not see any material advance in mental development until we go on to the Amphibia and Reptiles. There is

still greater advance when we come in the Mammals, though even here the minds of the Monotremes and of the typical Mammals remain at a low stage. But when we rise from these to the Primates we find without this one vast group such a number of important stages of differentiation and progress that the specific differences between the least intelligent (such as the apes) and the most intelligent Primates (such as the dogs and apes) are much greater than the specific differences between the lower Primates and the Mammals or Monotremes. Even certainly the differences are far greater than the difference in animal power between the dog, the ape, and man. Yet all these animals are genetically-related members of a single natural class.

We see this in a still more interesting aspect in the comparative psychology of another class of animals, that is especially interesting for early research—the insect class. It is well known that we find in many insects a degree of intelligence that is found in none else among the Vertebrates. Everybody knows of the famous communicative and social life of bees and ants, and of the very remarkable social arrangements in Hymenoptera, such as the bee among the more advanced types of ants, but among no other group of animals. I need only mention the social arrangements and government of the hymenopterous bees and the aphididae and ant-like insects that live different conditions—queens, dominators, workers, educators, soldiers, etc. One of the most remarkable phenomena in this very interesting portion is the mouth-clamping of the ants, which can clamp so tightly as will apparently extract their brooded pollen. Still more remarkable is the wire-holding of the large red ants, which bind the young of the small black ants and bring them up as slaves. It has long been known that these political and social arrangements of the ants are due to the different division of the functions existing, and that they understand each other. A number of recent observers, especially Fritz Müller, Sir J. Lubbock (Lord Avebury), and August Forel, have put the interesting degree of intelligence of these tiny Antecephala beyond question.

Now, compare with this the mind of many of the lower, especially the insect, forms, as Drosophila, *Tanypus*, the cockroach, the ant, the

(Class), which, in its adult state, has a conical, shield-shaped body, mounted on the base of plates. In fact we are asked. Its name is said to be the name of the plates of which it abounds in the egg. The whole psychia life of these little simple parsons exists in the plates they secrete from soaking the top of the plate and in equal measure with the plates. It is the same with the *Myriapoda* (the millipede & diplopoda), which spend their lives periodically and inconclusively, without wings or legs, in the abdication of change. There is a genuine love of higher psychic nature. We compare these sluggish parasites with the intelligent and active ants, we might add that the psychic differences between them are much greater than the psychic differences between the *Myriapoda* and insects, between the *Mollusca*, *Thermopoda*, and *Crustacea* at the one end and the dog, cat, or man at the other. Yet all these insects belong to the same class of Anthropodians as all the mammals living to-day fall to the same class. And just as every vertebrate organism must admit a certain continuity for all these insects so he must do for all the mammals.

If we now turn from the comparative study of psychia life in different animals to the question of the origins of the nervous system, we receive the answer that in all the higher animals they are always derived up with certain groups of cells, the great nerve cells or neurons that comprise the nervous system. All vertebrates & almost invertebrates are agreed that the central nervous system is the origin of psychia life in the animal, and it is possible to prove this experimentally at any moment. When we partially or wholly destroy the central nervous system, we according to its more proportion, partially or wholly, the "seed" or psychic activity of the animal. We have, therefore, to consider the sources of the psychic organs in man. The reader already knows the inextricable answer to this question. Man's psychic organ is, in structure and origin, not the same organ as in all the other vertebrates. It originates in the shape of a simple ganglion cells from the outer membranes of the embryo—the chorion layer. The simple cerebral vesicle that is formed by the expansion of the head-part of the embryonic tube divides by transverse convolution into five, and these five though none of them are

of importance in the human embryo as in the rest of the vertebrates. As these are situated at a certain angle, they divide and split and soon also have a common point.

Physiology teaches us further, as the result of observation and experiment, that the relation of the "seed" to the organ, the brain and spinal cord, is just the same as in the other mammals. They are distinct yet at all times the other; it is just as much bound up with it as another movement is with the shoulder. It can only develop in connection with it. If we are not informed at all, and grant the mutual immutability of neurogenesis and phylogeny, we are forced to admit this thesis: The human seed of psyche, as a function of the nervous tube, has developed along with it, and just as brain and spinal cord are derived from the ectopic mandibular tube in every human being also, is the human mind or the psychic side of the whole human race the true gradually evolved from the lower vertebrates people. Just as today the intricate structure of the brain proceeds step by step from the lower mammals at every human child class—the same five cerebral lobes—so in all the other Crustacea, as the human head has been gradually developed in the course of millions of years there a long series of intermediate forms, just as today an average human embryo the various parts of the brain differentiate into the typical type of the apes, bears, or the human psyche has gradually developed from the apes and monkeys.

It is true that the Mammal evolution is reported only human by most men, and the *Deutsche Presse*, which shows the inexpressible connection of brain and world, and regards body and soul as two totally different things, is still popular. But how are we to reconcile this view with the higher law of evolution? I repeat with different emphasis great and inexpressible at embryology and in phylogeny. If we compare with the majority of men the idea was in no impressionable body, which has nothing to do with the body itself, but nervous intuition is for a time given expression to his impressions through the brain just as the pencil does through his instrument. we must accept a point of human embryology at which the soul enters into the brain; and at such point we shall judge a creature of which it abandons the body. As further, such human individual has inherited certain

mental sources from each parent, we may suppose that in the act of conception the parents were separated from their souls and transferred to the embryo. A piece of the paternal soul goes with the spermatozoon, and a piece of the maternal soul remains in the ovule. At the moment of conception, when portions of the two souls of the approaching cells join together to form the nucleus of the embryo, the complementary fragments of the immortal souls must also be supposed to unite.

On this Dualistic view the phenomena of psychic development are simply incomprehensible. Everybody knows that the new-born child has no consciousness, no knowledge of itself and the surrounding world. In my present wife has frequently observed the mental development of his children will find it impossible to deny that it is a case of biological evolutionary processes. Just as all other functions of the body develop in connection with their organs, so the soul does its connection with the brain. The gradual unfolding of the soul of the child is, in fact, as wonderful and glorious a phenomenon that every mother or father who has eyes to observe is never tired of contemplating it. It is only our ignorance of psychology that keeps nothing of this development. We are almost compelled to think sometimes that their parents can never have had children themselves. The human soul, as described in some of our physiological works, is simply the soul of a learned philosopher, who has read a good theory book, but knows nothing of existence, and never or at no reflects that his own soul has had a development.

When these Dualistic philosophers are consistent they state enough & correct in the phylogeny of the human soul, of which it was first "introduced" into man's vertebrate body. Hence, at the time when the human body was evolved from the anthropoid body of the age (probably in the Tertiary period), a specific human psychic element—or, as people love to say, "a spark of divinity"—must have been suddenly infused or transplanted into the anthropoid brain, and been connected with the animal soul already present in it. I need not insist on the enormous theoretical difficulties of this idea. I will only point out that this "spark of divinity," which is supposed to distinguish the soul of man from that of the older animals, must be itself capable of development,

and has, as a matter of fact, progressively developed in the course of human history. As a rule, reference is taken to be this "spark of divinity," and is supposed to be the exclusive possession of humanity. But comparative psychology shows us that it is quite impossible to set up this barrier between man and the higher animals. When we take the word "manus" in the wider sense, and then it is found in the higher mammals, frog, dog, elephant, having just as well as at most now, a soul in the narrower sense, and then it is holding in more men just as weak as in the majority of animals. On the whole, we may add, say of man's soul what Goethe's Magdalene sang:—

Life sometimes better night captures him,  
But for the glories of blinding light the  
True soul gives him.  
He casts it down; then his power's  
consumed  
To be still weaker than ever he'd.

It is, then, we must reject these popular and, at times, respectable Dualistic theories as untenable, because incompatible with the genetic facts. There remains only the opposite or Monistic conception according to which the human soul in this very same animal soul, a division of the central nervous system, and develops in inseparable connection therewith. We say this independently in every child. The biological law compels us to affirm it physiologically. Just as in every human embryo the shadowy logic given rise to the voluntary acts, from the inferior end of which the five numbered vehicles of the Vedic deities are developed, and from these the numerous kinds (first with the characters of the lower, then with those of the higher animals); and as the whole of this ontogenetic process is only a brief, involuntary reproduction of the same process in the phylogeny of the Vertebrates; so the wonderful spiritual life of the human race through many thousands of years has been evolved step by step from the lowly psychic life of the lower Vertebrates, and the development of every child-man is only a brief repetition of that long and complex phylogenetic process. From all these facts round, reason must conclude that the still prevalent belief in the immortality of the soul is an untenable superstition. I have shown its inconsistency with modern science in the eleventh chapter of *The Soul of the Universe*.

Now it may also be well to point out

the great importance of anthropogeny, in the light of the diagnostic law, for the progress of philosophy. The anthropogenetic philosopher who takes cognizance of these anthropogenetic facts, and explains them in accordance with the law phylogenetically, will advance the great questions of philosophy far more than the most distinguished thinkers of all ages have yet succeeded in doing. Most certainly every observer convinced whether man derives from the facts of comparative anatomy and ontogeny we have adduced a number of suggestive ideas that cannot fail to have an influence on the progress of philosophy. Nor can it be denied that the sound statement and impartial appreciation of these facts will tend to the desirable triumph of the philosophical tendency that we call "Material," or "Mechanistic," as opposed to the "Dualistic" or "Spiritual," on which most of the ancient, confused, and modern systems of philosophy are based. The Material or Mechanistic philosophy affirms that all the phenomena of human life and of the rest of nature are ruled by fixed and unchangeable laws; that there is everywhere a necessary causal connection of phenomena; and that, therefore, the whole knowable universe is a harmonious unity, a system. It says, further, that all phenomena are due solely to manifested or efficient causes, and to final causes. Is this not indeed absurd in the ordinary sense of the word. In the light of the Mechanistic philosophy the phenomena that we are wont to regard as the free and most independent, the symptoms of the human will, are subject just as much to rigid laws as any other natural phenomena. As a matter of fact, important and thorough examination of our "free-will" shows that they are never really free, but always determined by antecedent factors that can be traced to either heredity or education. We cannot, therefore, admit the conventional distinction between nature and spirit. There is spirit everywhere in nature, and we know of no spirit outside of nature. Hence, the common wisdom of natural science and mental or moral science is blundering. Every action, we teach, is both natural and moral. That is a true principle of Mechanism, which, on its religious side, we may also demonstrate. Man is not alone, but he is.

It is true that the opponents of mechani-

stic laws to disprove the Mechanistic philosophy based on it, as "Materialism," and confute the philosophical tendency of this name with a wholly unwaranted and despotic moral accusation. Strictly speaking, it would be just to prove as such our system Spiritualism or Mechanism. The real Mechanistic philosophy affirms that the phenomena of life are like all other phenomena, effects or products of matter. The opposite carries, the Spiritualistic philosophy, says, on the contrary, that matter is a product of energy, and that all material forms are produced by free and independent force. Thus, according to mechanistic Mechanism, the matter is omnipotent as the First Cause; according to the equally absurd view of the Spiritualist, it is the reverse. Both views are Dualistic, and, in my opinion, both are false. For us the only dualism disappears in the Mechanistic philosophy, which leaves neither matter without force nor force without matter. It is only necessary to reflect for some time over the question from the metaphysical point of view to see that it is impossible to form a clear idea of either hypothesis. As Leibnitz said, "Matter does never exist in act without spirit, nor spirit without matter."

The human "spirit" or "soul" is surely a force or force of energy, incomparably bound up with the material substance of the body. The thinking force of the mind is just as much connected with the material elements of the brain as the motor force of the muscle with their structural elements. Our mental powers are functions of the brain as much as any other force is a function of a material body. We know of no matter that is dead, or free, and no forces that are not bound up with matter. When the forces enter into the phenomenon as constituents we call them living or active forces; when they are in a state of rest or inertiæ we call them latent or potential. This applies equally to mineral and organic bodies. The oxygen that connects iron filings, the powder that explodes, the waves that drive the human heart, are living energies. They act by strong force as much as the simplest magnet does when it attracts the iron at rest, or the opposite Attractives that break heart in the wind of the sea, or pass when the clouds. Only in the later case the attractions of the different forces that appear as "atmosphere" in the

*homogenes* are much more intricate and difficult to analyze than in the former.

Our study has led us to the conclusion that in the whole evolution of man, in his embryology and in his phylogeny, there are no living forces at work other than those of the two of organic and inorganic nature. All the forces that are operative in it could be reduced in the ultimate analysis to growth, the fundamental evolutionary factor that brings about the forms of both the organic and the inorganic. His growth itself depends on the interaction and regulation of homogeneous and heterogeneous principles, twenty-five years ago Carl Kraus summed up the general result of his famous study of animal development as he follows: "The evolution of the individual is the history of the growth of individuality in every respect." And if we go deeper in the root of the law of growth, we find that in the long run it can always be reduced to that attraction and repulsion of associated atoms which I have called the "born and borned" of the Universe.

Thus the evolution of man is governed by the same "natural law" as the development of any other body. There have always been in both the same simple principles, the elementary principles of physics and chemistry. The various phenomena of nature only differ in the degree of complexity in which the different forces work together. Such simple process of adaptation and heredity in the constitution of our ancestors is at least a very primitive physiological phenomenon. Far more intricate are the processes of human embryology, so these are understood and explained elements of the phylogenetic process.

In my *General Morphology*, which appeared in 1888, I made the first attempt to apply the theory of evolution, as reformed by Darwin, to the whole problem of Biology, and especially to provide with its assistance a mechanism of foundation for the science of organic forms. The author's relatives that exist between all sorts of organic species, especially the great causal series between the two entities of evolution—embryology and phylogeny—were explained in that work for the first time by transformation, and were interpreted phylogenetically in the light of the theory of descent. The embryological part of the *General Morphology* (first vol.) contains the best example to

determine the series of man's ancestry (vol. 5, p. 449). However important this attempt had, it provided a starting point for further investigation. In the thirty years that have since elapsed the biological horizon has been immensely widened, our improved apparatus in paleontology, comparative anatomy, and embryology have given us an astonishing amount. Owing to the united efforts of a number of able workers and the emanations of newer methods, many important biological questions that have appeared to be obscure enough seem to be clearly settled. Interpretation covers the scope of a new day of pure biology, namely, over the dual aspect of organic organization, and we find now, finally, and finally, that there is Daylight in our field of inquiry.

Philosophers and others, who are greatly ignorant of the empirical results of our ethnology and the phylogenetic methods of reducing it, have often freely claimed that in the matter of manufacturing and propagating new working men had been done than the discovery of "old" science, such as we had in the question of the sapient. This would be just true if the pathology given in the second part of this work were merely the interpretation of a series of normal forms of which we gathered the generic distinctions from their external morphological considerations. As we have sufficiently proved already, it is far as a question of a totally different thing—if the morphological and historical part of the physiology describes a class of these elements as the basis of their identity in historical stages and embryonic development; and I think I have sufficiently shown in the first part of this work how far this is extended to reveal to us their interrelations and the historical development. It was the excess of no significance residing in the word of historical connection, nor one of those scientists who believe in a real "cultural history," and who think a want of an historical knowledge of the past as of an equal investigation of the present. The individual value of the historical consciousness cannot be sufficiently emphasized at a time when historical research is limited and imperfect, and when an "exact" science, as degenerate as it is narrow, would suffice for a physical experiments and mathematical geometry. Historical history cannot be replaced by any other branch of science.

It is clear that the prejudices that stand in the way of a general recognition of this "natural anthropology" are still very great; otherwise the long struggle of philosophic systems would have ended in favour of Monism. But we may confidently expect that a more general acquaintance with the genetic facts will gradually destroy these prejudices, and lead to the triumph of the natural conception of "man's place in nature." When we hear it said, in face of this expectation, that this would lead to retrogression in the intellectual and moral development of mankind, I cannot refrain from saying that, in my opinion, it will be just the reverse; that it will promote

to an enormous extent the advance of the human mind. All progress in our knowledge of truth means an advance in the higher cultivation of the human intelligence; and all progress in its application to practical life involves a corresponding improvement of morality. The worst enemies of the human race—ignorance and superstition—can only be vanquished by truth and reason. In any case, I hope and desire to have convinced the reader of these chapters that the true scientific conprehension of the human frame can only be attained in the way that we recognize to be the solo sound and effective one in organic science generally—namely, the way of Evolution.

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